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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 13. SYSTEMATICS AND PHYLOGENETIC PATTERN OF EARLY EOCENE *HYOPSODUS* (MAMMALIA: CONDYLARTHRA)

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Abstract

Hyopsodus is the most common Eocene mammal in western North America, making it an excellent candidate for the study of evolutionary change in a mammalian genus through time. Analysis of numerous dental specimens of Wasatchian and early Bridgerian age indicates that considerable variation existed within what are considered here species of the genus. The nature and pattern of this variation were assessed by evaluation of dental characters and size among specimens that were separated by relative temporal age. This approach led to the identification of two anagenetically evolving "species lineages"—that is, lineages of *Hyopsodus* that demonstrate directional shifts in the frequency and degree of character expression through time. These lineages are *Hyopsodus paulus* (intermediate-sized and spanning most of the Eocene) and the larger *Hyopsodus powellianus* (present from the middle early Eocene through the earliest middle Eocene). Species lineages are divided into successive, informal segments in order to reflect relative age and morphologic differences. Three other small-sized taxa show relationship to *Hyopsodus paulus* at different times during the lineage's history. From oldest through youngest, these species are *Hyopsodus loomisi, Hyopsodus minor,* and *Hyopsodus minusculus. Hyopsodus loomisi* and *Hyopsodus minor* may also represent a lineage. One other taxon, *Hyopsodus* sp., cf. *H. mentalis,* is present in the early Eocene of New Mexico and, apparently, Wyoming. However, its relationship to other *Hyopsodus* and its geographic distribution remain poorly understood. Naming lineages and branches of lineages or cladistically resolving relationships using conventional systematic approaches is difficult because of the fundamental difference between Recent and fossil species.

Introduction

Hyopsodus (Figure 1) is one of the most ubiquitous Eocene mammalian genera; collections throughout the United States boast thousands of dental remains, usually isolated teeth and maxilla or mandible fragments. In comparison to dentitions, postcranial material is surprisingly rare. Gazin (1968) gives an excellent comparative survey of *Hyopsodus* postcranial material.

Most *Hyopsodus* were probably no more than 30 cm in length with an elongate body plan—vaguely like the modern ermine (Gazin, 1968). *Hyopsodus* retains the primitive full eutherian complement of teeth, yet the semicrescentic pattern of the molar cusps and lophs is unique. The limbs are relatively short and unspecialized and the anterior incisors somewhat large; suggesting to some a partly arboreal, omnivorous niche (Matthew, 1915*a*) or, alternatively, a more fossorial habit (Gingerich, 1974*a*). These questions aside, *Hyopsodus* must have often been a major constituent of North American Eocene faunas.

No derived appendicular or dental characters definitively suggest a relationship between *Hyopsodus* and any of the modern orders of mammals. *Hyopsodus* continues to be consistently referred to the paraphyletic order Condylarthra. Previously it had been considered an ungulate (Cope, 1875; Abel and Cook, 1925), a

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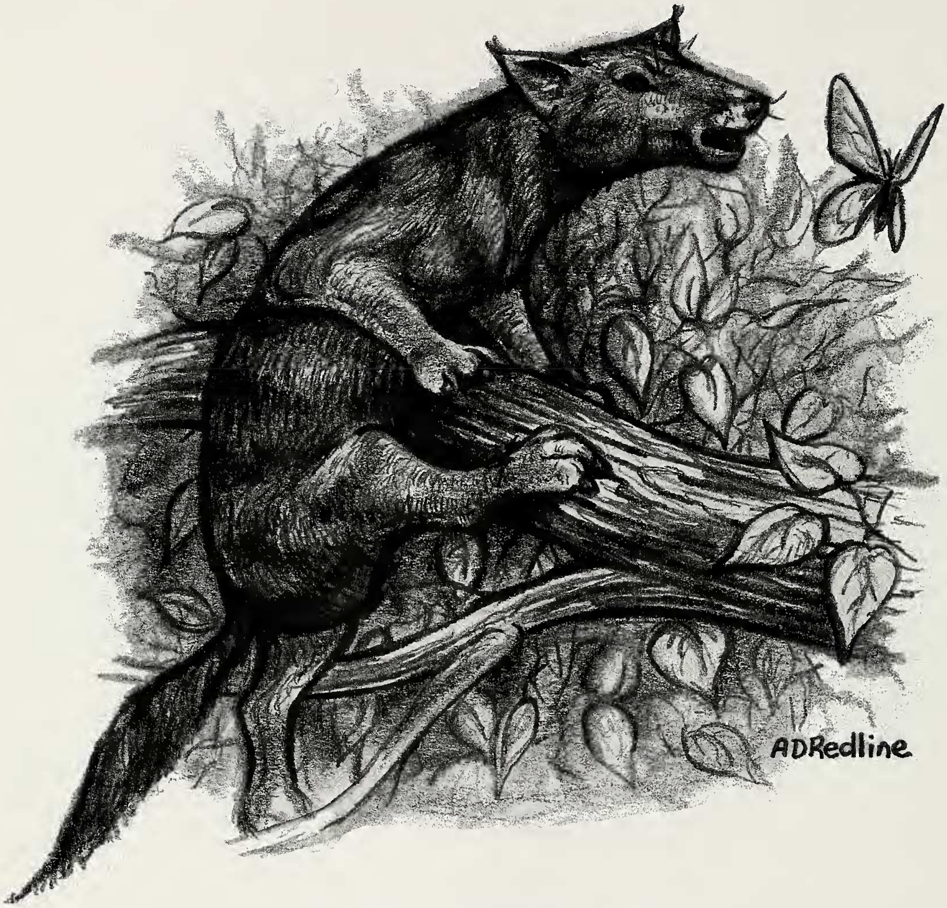

Fig. 1.—Restoration of *Hyopsodus.*

primate (Marsh, 1875; Schlosser, 1887; Matthew, 1899) or close to the Insectivora (Lydekker, 1885; Wortman, 1903; Loomis, 1905).

Matthew (1915*a,* 1915*b*) placed *Hyopsodus* within his emended order Condylarthra (essentially as used today but excluding the Periptychidae), corroborating Pavlow's (1887) preliminary observations. Simpson (1937) included periptychids in the Condylarthra and placed many Paleocene genera within the family Hyopsodontidae, a classification maintained in his 1945 monograph on mammalian systematics. Van Valen (1978) has since separated the hyopsodontids from the mioclaeneids, both considered subfamilies of the Hyopsodontidae by Simpson. Hyopsodontid resemblances to artiodactyls (e.g., Simpson, 1937:231) and South American "ungulates" (Paula Couto, 1952) have also been noted. Cifelli's (1982) study on condylarth petrosal structure does not appear to support these or other suggested affinities, at least among the genera examined. Condylarth systematics remain stifled by the lack of skull, anterior dentitions, and postcranial material for many genera. Of the North American Paleocene hyopsodontids, "*Aletodon*" *quadravus* (Gingerich, 1983) (but not *A. gunnelli* of Gingerich, 1977) may be dentally most similar to *Hyopsodus,* more so than *Haplomylus,* which has traditionally been allied with *Hyopsodus* (Van Valen, 1978). The relationship of *Hyopsodus* to other condylarths remains unclear and will not be understood until a comprehensive review of the condylarths is undertaken.

Hyopsodus first occurs in the latest Paleocene (Clarkforkian Land Mammal Age; see Rose, 1981) and by the early Eocene is either the most common or one of the most common North American mammalian faunal elements. *Hyopsodus* decreases in numerical prominence after Bridgerian time but persists through the Uintan. One species, *Hyopsodus sholemi,* is found at the ?Duchesnean Shoddy Springs locality (see Krishtalka, 1979, for the most recent revision of later Eocene *Hyopsodus*).

Robinson (1966:54) called *Hyopsodus* taxonomy a "systematist's nightmare." *Hyopsodus* material is so abundant and its occurrence in faunas so pervasive that it is difficult to assess the morphologic variability or relationships of species unless stratigraphically detailed analysis is performed. The last comprehensive review of *Hyopsodus* was Gazin's 1968 monograph, a study that considerably simplified the systematics of the genus. However, the taxonomic criteria he used consisted of little more than molar length reckoned with prevailing species nomenclature. Additionally, the stratigraphic resolution of the collections examined was relatively coarse by modern standards. Unfortunately, many of the older collections, although very large, simply lack the precise (or accurate, in some cases) locality data necessary for systematic or evolutionary study. Systematic revision is also hampered because most type specimens lack this information. More recent work with *Hyopsodus,* although stratigraphically sound, has dismissed dental characters (aside from size) and their variation.

As stated by Bown and Rose (1987), " . . . there has been no published study of dental morphology and dental variability in *Hyopsodus* since Gazin's (1968) work, and very little there." Recent (1975–1990) collections of *Hyopsodus* made by the Carnegie Museum of Natural History, Texas Tech University, and the University of Colorado, Boulder, from the Wind River Basin, Wyoming, and, to a lesser degree, the San Juan (New Mexico) and Bighorn (Wyoming) basins, have much better stratigraphic control. This new material allows a reevaluation of not only the systematics and dental variability of early Eocene *Hyopsodus,* but also of its pattern of evolution. Given the abundance of fossil material, an analysis of *Hyopsodus* should shed new light on these questions and possibly even indicate whether these questions are appropriate.

Abbreviations used in text and tables are as follows: Institutional: ACM—Amherst College Museum, Amherst, Massachusetts; AMNH—American Museum of Natural History, New York, New York; ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania; CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; UCM—University of Colorado Museum, Boulder, Colorado; UCMP—University of California Museum of Paleontology, Berkeley, California; USNM—United States National Museum, Washington, D.C.; UW—University of Wyoming, Laramie, Wyoming.

PREVIOUS INVESTIGATIONS

Hyopsodus, since its initial description in 1870 (Leidy), has had an interesting and somewhat confusing history of investigation. Problems have included lack of stratigraphic control in many early collections, lost type specimens, and the misconception that the dentition of *Hyopsodus* is so variable in morphology that distinction of species is impossible (Gazin, 1968:16; Gingerich, 1974*a*:107; West, 1979*a*:4). The latter opinion has caused the most recent work on *Hyopsodus* to be primarily statistical in nature.

This study focuses on the systematics and phylogenetic pattern of early Eocene *Hyopsodus* (Wasatchian through earliest Bridgerian Land Mammal Ages). A history of the taxonomy of Wasatchian and early Bridgerian *Hyopsodus* is given in Table 1. A more thorough history of investigation of *Hyopsodus* is provided by Gazin (1968).

The species listed in Table 1 have been subject to various revisions within the last century. A history of revision is given here in an attempt to reintroduce species and remarks on their morphology that have been subsequently ignored or forgotten.

Bridgerian *Hyopsodus* was revised by Matthew (1909) who described its postcranial anatomy for the first time. He synonymized *Hyopsodus vicarius* with *H. paulus,* and described as new the skull of *Hyopsodus despiciens,* which he suggested was the same species as Osborn's (1902) skull of *H. paulus* from the Washakie Basin.

In 1915(*b*), Matthew recognized Loomis' *Hyopsodus simplex* as characteristic of Sand Coulee beds and the somewhat younger "Gray Bull" horizons of the Bighorn Basin. Characters he considered diagnostic included comparatively small third molars, weak hypocones on M^1 and M^2, and weaker premolar cingula.

In the same paper, Matthew designated topotypes for both *H. mentalis* and *H. miticulus,* as the holotypes were already missing. *Hyopsodus miticulus* was retained for specimens from the San Juan Basin and material larger than *Hyopsodus simplex* from the Gray Bull. Matthew noticed a somewhat stronger hypocone in *H. miticulus* as well as a more quadrate exterior cone (paracone) on P^4. Collections of dental remains of this species were already large and Matthew commented on the variability of many tooth characters in *Hyopsodus miticulus.* Matthew also retained Cope's *Hyopsodus mentalis* from the Largo beds of the San Juan Basin and considered *Hyopsodus lemoinianus* to be conspecific with it. Larger size (compared to *H. miticulus*) was cited as chiefly diagnostic of this species, although other characters given by Matthew include a distinct entoconid and hypoconulid on M_3, large hypocones on M^{1-2}, and a large external cone on P^{1-3}. Lower molars of this species were described as being more elongate. Matthew used *Hyopsodus mentalis* for intermediate-sized individuals (smaller than *H. powellianus,* larger than *H. minor* and *H. minusculus*) from the Lost Cabin zone of the Wind River Basin and from upper beds of the Bighorn Basin. A more detailed tracking of change in variability through time was severely constrained by an inadequate biostratigraphic framework.

Matthew named the new subspecies *Hyopsodus mentalis lysitensis* for specimens from the Wind River Lysite that he regarded as "intermediate in size and progressiveness" between *H. miticulus* and *H. mentalis* (both of the latter species were known to be lithosympatric in the San Juan beds).

Matthew applied *Hyopsodus wortmani* to small *Hyopsodus* from the Wind River Lost Cabin beds; very small Lysite specimens were assigned to the subspecies *H. wortmani minor.* He also commented on the probable relationship of *Hyopsodus mentalis* and *Hyopsodus wortmani* to the Bridger forms *H. paulus* and *H. minusculus,* a logical conclusion that has not been considered in the recent literature (see Gazin, 1968, and West, 1979*a*). Matthew mentioned the "progressive"

Table 1.—Chronologic summary of the named species of *Hyopsodus* from Wasatchian and early Bridgerian strata. Biostratigraphic age of type is listed.

North America

1. *Hyopsodus paulus*—Leidy, 1870. Type species. Type specimen probably Blacksforkian in age.
2. *Hyopsodus gracilis*—(Marsh, 1871). Transerred to *Microsyops* (Leidy, 1872) and *Notharctus* (Cope, 1872). Later made type species of *Smilodectes* (Wortman, 1903). Specimen Blackforkian in age.
3. *Hyopsodus minusculus*—Leidy, 1873. Type specimen Blacksforkian in age.
4. *Hyopsodus vicarius*—(Cope, 1875). First described as *Microsyops vicarius* (Cope, 1873). Type specimen Twinbuttean in age.
5. *Hyopsodus miticulus*—(Cope, 1877). First described as *Esthonyx miticulus* (Cope, 1874). Type specimen from San Juan Basin, Wasatchian in age. Specimen lost.
6. *Hyopsodus mentalis*—(Cope, 1877). First described as *Antiacodon mentalis* (Cope, 1875). Type specimen from San Juan Basin, Wastachian in age. Specimen lost.
7. *Hyopsodus speirianus*—(Cope, 1880*b*). Made the type species of *Haplomylus* (Matthew, 1915*b*).
8. *Hyopsodus lemoinianus*—(Cope 1882*a*). Type specimen from Bighorn Basin, probably Lysitean in age.
9. *Hyopsodus powellianus*—Cope, 1884. Type specimen from Bighorn Basin, probably Lysitean in age.
10. *Hyopsodus wortmani*—(Osborn, 1902). Type specimen from Wind River Basin, probably Lostcabinian in age.
11. *Hyopsodus simplex*—(Loomis, 1905). Type specimen bears label "Tatman Mountain." Graybullian or Sandcouleean in age.
12. *Hyopsodus minor*—Loomis, 1905. Type specimen from Wind River Basin, Lysitean in age.
13. *Hyopsodus browni, H. lawsoni, H. jacksoni*—(Loomis, 1905). Specimens from Wind River Basin, Lysitean in age.
14. *Hyopsodus walcottianus*—(Matthew, 1915*b*). Type specimen from Wind River Formation, probably Lostcabinian in age.
15. *Hyopsodus latidens*—(Denison, 1937). Type specimen from Indian Meadows Formation, northeastern Wind River Basin, Wasatchian in age.
16. *Hyopsodus loomisi*—McKenna, 1960. Type specimen from northwestern Colorado Four Mile locality, Sandcouleean in age.
17. *Hyopsodus pauxillus*—Gingerish, 1994. Type from Wasatchian 5 interval, Clark's Fork Basin, Graybullian in age.

Europe and Asia

1. *Hyopsodus jurensis*—(Rutimeyer, 1891). Specimens referred to Dichobunidae by Schlosser (1894) and Stehlin (1906). From the Eocene of Switzerland.
2. *Hyopsodus orientalis*—Dashzeveg, 1977. From Eocene beds of Mongolia.
3. *Hyopsodus wardi*—Hooker, 1979. Type specimen from Eocene Blackheath beds of England.
4. *Hyopsodus itinerans*—Godinot, 1981. Type specimen from Eocene Rians region of France.

nature of the fourth upper and lower premolars of *Hyopsodus wortmani,* but only in comparison with older Gray Bull *H. miticulus.*

Also in this review, Matthew named the species *Hyopsodus walcottianus* from the Wind River Lost Cabin and allied it with the somewhat smaller (but still large) Lysite taxa *Hyopsodus powellianus* and *H. powellianus browni.*

Kelley and Wood (1954) revised the Wind River Lysite record of *Hyopsodus* as part of a review of the Lysite fauna. Their analysis involved statistically testing four populations defined by morphology. The results indicated the presence of two commonly occurring taxa: *Hyopsodus powellianus* (including *H. jacksoni* and *H. browni*) and *Hyopsodus mentalis.* The holotype and, apparently, the only specimen of *Hyopsodus minor* was retained as a discrete species based on its extremely small size. *Hyopsodus minor* was not considered to be a subspecies of *H. wortmani,* differing from Matthew's (1915*b*) conclusions. Kelley and Wood held that *Hyopsodus mentalis* specimens were variable, with some resembling the type (probably a topotype) and others approaching *H. wortmani,* although no characters were given.

Kelley and Wood also noted other dental variations in *Hyopsodus.* In *Hyopsodus mentalis,* these included the presence of a P_4 metaconid, prominence of the hypoconid on P_4, and strength of the lower molar paraconid. In *Hyopsodus powellianus* the P_4 metaconid was said to be variably strong, as was the molar paraconid. M_3s of *Hyopsodus powellianus* were shown to exhibit highly variable heel development, with the hypoconulid differing in size and its consequent effect on the structure of the molar talonid.

Kelley and Wood (1954) reiterated Matthew's reservations that specimens of *H. powellianus* from the Wind River Basin were smaller than those from the Bighorn Basin, but did not use Matthew's subspecies designations for the Wind River material.

The earliest Wasatchian record of *Hyopsodus,* as reported by McKenna (1960), consisted of two species—*H. miticulus* and a new smaller species that he named *Hyopsodus loomisi. Hyopsodus loomisi* included some specimens referred by Loomis (1905) and Denison (1937) to *Hyopsodus simplex* (from the Bighorn Sand Coulee beds and the Indian Meadows Formation, respectively). According to McKenna, the formal diagnosis of *H. simplex* described variability typical of both *H. miticulus* and *H. loomisi,* hence they could not be discriminated based on lower dentitions. Since the stratigraphic provenance of the type of *H. simplex* is incompletely recorded, McKenna hesitated in using it as comparative material for earliest Eocene *Hyopsodus. Hyopsodus simplex* was recorded by Loomis as being collected from Sand Coulee beds, but Matthew (1915*b*) and Denison (1937) state that the type is actually from significantly higher strata, within the Graybull beds. McKenna suggested that lower molar proportions and P_4 paraconid development do not distinguish *H. simplex* from *H. miticulus.* McKenna strengthened the case of dismissing *Hyopsodus simplex* by stating that the type differed from the referred specimens in featuring well-developed entostylids and a multicusped M_3 talonid heel.

As mentioned earlier, Gazin (1968) provided the only recent comprehensive review of the species of *Hyopsodus.* Most of his data relevant to systematic review consists of histograms of the measured length of the lower second molar. The collections available at the time were tied to the known biostratigraphic record. As Cope's San Juan Basin taxonomy had priority, Gazin applied it in constructing a systematic framework for Wasatchian *Hyopsodus.* Significantly, Gazin synonymized *Hyopsodus mentalis* with *Hyopsodus miticulus* and referred to the latter all intermediate-sized *Hyopsodus* species from the entire Wasatchian, including *Hyopsodus simplex* and *Hyopsodus lemoinianus* (from the Bighorn Basin), Matthew's *H. mentalis lysitensis* (Lysite Member of the Wind River Formation), and *Hyopsodus latidens* (Denison, 1937). Gazin assigned small specimens to *Hyopsodus wortmani* except for those from the very earliest Wasatchian. Thus, *H.*

wortmani was seen by him to encompass material from the Wind River, Buffalo, Green River, Bighorn, and Huerfano basins, including the Lysite record of *Hyopsodus minor.* However, the small *Hyopsodus loomisi* from the Sand Coulee beds was retained due to its more primitive molar structure.

For resolving large-sized *Hyopsodus,* Gazin retained some subspecies designations for geographical variants. *Hyopsodus powellianus* was maintained for large specimens from Lysitean strata of the Bighorn Basin, with the smaller subspecies *H. powellianus browni* (Matthew, 1915*b*) recognized in the Lysite Member of the Wind River Formation. Lost Cabin Member specimens were referred to *Hyopsodus walcottianus,* chiefly on the basis of their larger size.

Gazin's review of early Bridgerian species was more straightforward, and he allocated all intermediate-sized material to *Hyopsodus paulus* (Leidy, 1870). The type of *H. paulus* is probably from Bridger B strata and is extremely numerous in all Blacksforkian deposits. *Hyopsodus minusculus* was retained as a small species. Gazin also recognized these species at Powder Wash (Utah). Gazin noted that in the late Bridgerian Twin Buttes horizons these two species do not commonly occur together; only an intermediate lineage is present in early Bridger C (also noted by West, 1979*b*).

At the time of Gazin's (1968) review, 17 species of Wasatchian and early Bridgerian *Hyopsodus* had been proposed in the literature. He reduced these to seven, with some possible subspecies present in discrete geographic areas. Two European species, probably of early Eocene age, have since been added (Hooker, 1979; Godinot, 1981). Within this more stable taxonomic framework, recent work has begun to document the rate and pattern of *Hyopsodus* evolution.

Gingerich (1974*a*) employed the early Eocene record of *Hyopsodus* in a stratophenetic analysis supportive of gradual evolution. Although not specifically a revision of the genus, Gingerich dealt with *Hyopsodus* lineages from tightly controlled stratigraphic sequences ranging from the earliest Wasatchian through the earliest Lostcabinian of the Willwood Formation. All of these lineages were defined by graphically plotting $\log_{10}$ of the product of length times width of the first lower molar, a practice defended elsewhere (Gingerich, 1974*b*). However, Gingerich's graphic portrayal of these data suffers from some conceptual drawbacks. In order to follow this method, the investigator must make *a priori* decisions about the acceptable variation of a category—in this case, size-defined taxa of *Hyopsodus.* As Gingerich's figure (1974*a*:14, fig. 1) suggests, some of the lineages from different horizons range widely in variation about the mean. In some cases they are arbitrarily split into two clusters representing two taxa; in other cases, this range is lumped into one taxon. Single specimens, that in other horizons could be easily incorporated into a population range, are sometimes isolated as "forerunners" of later emerging taxa. Since the $\log_{10}$ length/width operation must be performed after the data set (in this case, a *Hyopsodus* taxon) has already been defined, it is of little surprise that the resulting pattern is indicative of the original hypothesis.

Gingerich applied taxonomic names to his lineages. These included a *H. loomisi–H. miticulus–H. lysitensis–H. wortmani* lineage (early Graybullian through Lostcabinian), *H. simplex* (derived from *H. loomisi* in the Graybullian), a *H. latidens–H. minor* lineage derived from the main stem in late Graybullian times and persisting through the Lysitean, and the large-sized lineage *H. powellianus–H. walcottianus* (stemming from *H. lysitensis* in the mid-Lysitean). Mensural data, as cited by Gingerich, does not support an ancestor–descendant relationship between *Hyopsodus* *minor* and *Hyopsodus wortmani.* Gingerich speculated on the derivation of "*Hyopsodus mentalis,*" the intermediate-sized Lostcabinian species common in the Wind River Basin, from the large-sized "*Hyopsodus powellianus*" lineage. From the Willwood Formation there is very little data to support this hypothesis.

A similar stratophenetic approach was used in the examination of the Bridgerian *Hyopsodus* record (West, 1979*a,* 1979*b*), with evidence presented for a small-sized and an intermediate-sized lineage of *Hyopsodus* in Bridger B rocks. According to West, the proper species names are *Hyopsodus minusculus* (small) and *Hyopsodus paulus* (intermediate).

METHODS OF ANALYSIS

Specimens of *Hyopsodus* examined in this study are primarily from the large Carnegie Museum of Natural History Wind River Formation collections, and, to a lesser degree, from the Bighorn, Piceance, and San Juan basins. Some specific localities are discussed in the text. Land mammal ages and subages follow the definitions of Krishtalka et al. (1987).

The *Hyopsodus* material consists of upper and lower jaws and jaw fragments containing a dentition as well as isolated teeth. All specimens of *Hyopsodus* were examined by locality for the purposes of morphological discrimination of phena and quantitative data collection. Each of the CM Wind River Formation localities was subsequently assigned a relative temporal age as accurately as recent lithostratigraphic and biostratigraphic work within the basin makes possible. Specimens from outside the Wind River Basin were also examined comparatively, but in a less controlled stratigraphic context. Table 2 lists localities along with relative stratigraphic, chronologic, or assemblage position. Locality information is on file in the Section of Vertebrate Paleontology, Carnegie Museum of Natural History.

In this study, two complementary techniques were used primarily as methods of analysis. Specimens of *Hyopsodus* from the CM collections were sorted by locality. Data from older collections with less rigorous stratigraphic information were recorded, but were not mixed with data from more recent collections. Maximum occlusal tooth length and width were measured with a calibrated ocular micrometer mounted on a stereoscope. The contribution of cingula and trigonid/talonid shape to these measurements varies but is easily noticeable. Generally, the shape of teeth from any one locality does not differ in its effect on length and width measurements; if it does, it is usually indicative of a derived morphologic condition. Isolated teeth were sometimes measured if tooth position could be accurately assessed, especially in specimens from localities where jaw fragments are rare, such as the earliest Wasatchian Four Mile area. When possible, measurements of isolated molar teeth, with the exception of those from Four Mile, are not included in the histograms presented in this study because of the difficulty of discerning first and second lower molars. The above-mentioned histograms are of the length of the lower second molar plotted against number of individuals. This essentially duplicates the methods of Gazin (1968), and is appropriate for the following reasons: (1) most specimens preserve the lower second molar; (2) the isolated nature of most Wind River Basin exposures and the lack of precise stratigraphic information for the older CM collections from other basins make the adoption of a completely "stratophenetic" approach impractical. Even within the Wind River Formation, lateral sedimentological variation makes precise correlation difficult, especially at the basin margins (Soister, 1968; Stucky, 1984*a*); (3) the length of the second lower molar is the least variable simple measurement possible (Gazin, 1968; contra Gingerich, 1974*b*) and is determined relatively rapidly on numerous specimens; (4) direct comparison can be made to Gazin's large database; (5) data can be plotted easily without placing a specimen into a preconceived taxonomic group as Gingerich's (1974*a*) methods require. West (1979*b*) presented results from graphing $\log_{10}$ of length times width of the first lower molar against stratigraphic position, as well as length of M_2 against number of individuals from more coarsely defined intervals (e.g., Bridger B of USNM). In both cases, it is possible to determine the presence of two taxa.

A major objective of this study was to investigate dental morphology and its variation in species lineages (defined below) of *Hyopsodus.* Size is not the only determinant for recognizing taxa, contrary to much of the literature (Gazin, 1968; Gingerich, 1974*a*; West, 1979*a,* 1979*b*) concerning species of *Hyopsodus.* Therefore, specimens were examined for derived characters and character frequencies that could be used to discern taxa independently of size. Koch (1986) attributes change in tooth size (but not morphology) in the modern record to cline translocation due to the effects of temperature. Koch also investigated the Eocene record of *Hyopsodus* (using Gingerich's data) in an attempt to find similar patterns within the fossil record. Change in size through time was found to be greater than expected for a clinal translocation model. It seems that this investigation was hindered by an imperfect knowledge of the zoogeographic (as opposed to geologic) distribution of fossil taxa and of paleotemperature variability. Also, to the best of my knowledge, evolutionary pattern through time has not been demonstrated to have a direct relationship to geographic pattern at any specific time (see also Bown et al., 1994). This may be partly because biologic and paleontologic species are not comparable as they are not defined by the same criteria.

In this study, size is considered one part of the entire character complex that defines the individual. Specimens were assigned (and in many cases reassigned) to taxa primarily on morphologic grounds other than size. The validity of dental characters was then tested against size distribution. In many cases, there was agreement between allocations based on size and all other dental morphology. Using this agreement as an indicator of a valid taxon, it was possible to trace dental morphologies through relative time and subsequently discriminate taxa whose tooth sizes overlap considerably. Conversely, the legitimacy of character and character frequency statements were tested in the face of well-established size trends. After the emergence of some fairly consistent derived characters within lineages of *Hyopsodus,* it became more feasible to note the extent of variability expected within a taxonomic unit. An attempt is made to describe this variability and its overlap. From these data it was possible to construct an internally consistent classification of early Eocene Wind River Formation *Hyopsodus* and compare and refer specimens of *Hyopsodus* from other partly contemporaneous Western Interior basins to this classification. Until there is a consensus concerning the fossil species concept, an internally consistent classification may be one of the most attainable goals of a systematic review.

It was necessary to compare specimens from a wide variety of localities that differ in their stratigraphic or temporal control. For example, because most Gardnerbuttean specimens are from a single locality (Sullivan Ranch, CM loc. 34), it might be argued that these specimens would be expected to show less variability in size and morphology. Therefore, to facilitate comparison, data from the more numerous Lostcabinian localities are grouped together as well as analyzed separately in order to make more valid comparisons.

SYSTEMATICS OF EARLY EOCENE *HYOPSODUS*

In order to establish a useable classification, one applicable to all North American early Eocene localities, it was necessary to adopt a consistent philosophical stance. The systematic conclusions of this study are best understood with knowledge of this position, which is presented here. Preliminary results on the evolutionary pattern of *Hyopsodus* were summarized by Redline (1990*a*).

The use of a simplified stratigraphic analysis was adopted for two primary reasons. The statistical analyses of Gazin (1968), Gingerich (1974*a,* 1974*b,* 1976*a,* 1976*b*), and West (1979*a,* 1979*b*) suggest that size differences of molar teeth are indicative of some discrete taxa of *Hyopsodus.* Secondly, the morphological variation in upper and lower dentitions is of sufficient magnitude to warrant investigation of material from immediately younger and older strata in order to determine the pattern of evolutionary change and relationship. Detailed analyses of other early Eocene mammals (e.g., *Diacodexis*—Krishtalka and Stucky, 1985; omomyids—Bown and Rose, 1987) have begun to document the nature of evolutionary pattern and rate in other mammalian genera during this time period. Unfortunately, much of this information has been obscured by the search for a suitable nomenclatural solution to apply to the patterns that are apparent. While dental characters are more important than size distribution in diagnosing lineages of *Hyopsodus,* raw size data make an excellent framework for testing hypotheses of relationship. Because this study places a premium on large sample sizes from stratigraphically controlled localities, specimens from areas without adequate biostratigraphic detail were not treated in depth.

Preliminary work with *Hyopsodus* was complicated by difficulty in making taxonomic decisions about material from large collections without information regarding relative stratigraphic position. When specimens were treated in lithosympatric groups, it was discovered that many morphologic character states were normally distributed within clusters, whereas other characters were far more stable (either present or absent). When time (as indicated by biostratigraphy) is superimposed

Table 2.—*Listing of primary study localities.*

Wasatch Formation, northwestern Colorado.

Four Mile loc. CM 953.

Willwood Formation, Bighorn Basin, Wyoming.

J. L. Kay's Graybull localities. CM 140–157.
Hackberry Hollow. CM 878.
Dorsey Creek loc.

San Jose Formation, San Juan Basin, New Mexico.

Almagre. CM 941, 945, 1017–1019, 1021, 1907.
Largo. CM 1025–1027, 1030–1031, 1033.

Debeque Formation, Piceance Basin, Colorado.

Scenery Gulch loc.
Shooty Gulch loc.

Wind River Formation, Wind River Basin, Wyoming.

Cole 1 and 2. CM 1903, 1904.
Lysite Flats 1. CM 928.
Lysite Flats 1A. NW of CM 928.
Lysite Flats 2. CM 793.
Lysite Flats 3. CM 929.
Lysite Flats 3A. CM 930.
Lysite Flats 3B. CM 794.
Lysite Flats 4. CM 931.
Lysite Flats 5. CM 111.
Lysite Flats 6. CM 112.
Lysite Flats 7. CM 802.
Lysite Flats 8. CM 803.
Lysite Flats 9. CM 805.
Lysite Flats 10. CM 800.
Lysite Flats 11. CM 806.
Lysite Flats 13. CM 877.
Lysite Flats 14. CM 801.
Davis Draw A. CM 118.
Davis Draw B and C. CM 797.
Cedar Ridge 1. CM 964.
Cedar Ridge 2. CM 965.
Cedar Ridge 3. CM 966.
Fross Lysite 1. CM 927.
Fross Lysite 1A. CM 1007.
Fross Lysite 5 and 6. CM 1008–1009.
Lysite Rim localities. CM 807, 809–813, 1064, 1091.
Guthrie locality 6. CM 114.
Lysite Flats (nonspecific). CM 130.

Wind River Formation, Wind River Basin, Wyoming.

Okie Trail 1. CM 936.
Okie Trail 2. CM 1049.
Okie Trail 3. CM 1050.
Okie Trail 4. CM 1051.
Okie Trail 5. CM 858.
Viverravus Jaw loc. CM 1550.
Pavillion loc. CM 1952.

Table 2.—*Continued.*

Wind River Formation, Wind River Basin, Wyoming.
Moneta Hills 1. CM 1046.
Moneta Hills 2. CM 1047.
Moneta Hills 3. CM 1048.
Moneta Hills 4. CM 1541.
Moneta Hills 5N. CM 1534.
K-5. CM 1039.
K-5N. CM 856.
K-6 (two levels). CM 1040.
K-7, K-7E, and K-7W. CM 91, 1041, 1042.
K-8. CM 857.
K-9. CM 1043.
K-13 and K-14. CM 1076–1077.
Lost Cabin near Dubois. CM 99.
Rate Draw 1. CM 1959.
Muddy Creek. CM 1910.
Bridger Creek 1. CM 1542.
Wild Horse Butte. CM 1011.
Kay's Lost Cabin SE of Riverton loc.
Kay's Lost Cabin. CM 88.
Day Butte. CM 1908.
Guthrie Lost Cabin 4. CM 90.
Deadman Butte. CM 1551 (= UCM 80062).
Red Creek. UCM 79039.
UCM 80088.
UCM 79043.

Wind River Formation, Wind River Basin, Wyoming.
Sullivan Ranch (Guthrie loc. 1). CM 34 (two levels).
K-2. CM 1036.
K-4 (Train Butte loc.). CM 1038.
K-15E, K-15W. CM 1078, 1080.
Palaeosyops Jaw loc. CM 1548 (= UCM 81010).
Someday loc. CM 1545 (= UCM 79040).
Lightning Butte. CM 1543 (= UCM 80061).
Rainbow Butte. UCM 80065.
Sally's Catfish loc. UCM 80064.
UCM 81026.

onto these distributions, the resulting pattern shows discrete lineages of taxa that demonstrate shifts in frequencies and degrees of expression of morphologic characters through time. Anagenesis is strongly suggested as a cause of this pattern because much morphologic change seems to have occurred without an increase in total taxonomic diversity. This pattern of evolution is very similar to that observed in the early Eocene artiodactyl *Diacodexis* (Krishtalka and Stucky, 1985). The authors of that study used a unique nomenclatural scheme when revising *Diacodexis,* one that describes the phylogenetic pattern of *Hyopsodus* as well.

Hyphenated trinomials (species lineages of Krishtalka and Stucky, 1985) are employed as the most reasonable solution to early Eocene *Hyopsodus* systematics. Only species designations are formally applied, while the third part of the trinomial represents the achievement of an anagenetic grade of character expression by a majority of specimens from a biostratigraphic "population" (a central tendency). The third name of the trinomial is referred to as a segment. Since the nature of lineage transitions through time is often gradational, species-lineage segments are necessarily delineated arbitrarily. This problem is inherent; work with an extremely dense fossil record of *Hyopsodus* indicates the presence of morphological variation and overlap both between contemporaneous lineages and among lineage segments of the same species that differ in biostratigraphic age. Integrating time and taxonomy in this manner suggests that true biological species have little reality when divorced from the conditions of synchroneity. Given the lack of any knowledge concerning the population genetics of fossil taxa, species-lineage systematics also avoids the problematic and debatable implications of subspecies. Subspecies are firmly rooted in neontology and zoogeography, disciplines dealing with synchronous phenomena.

Lineages furthermore provide a useful conceptual framework for visualizing the iterative evolution of derived taxa from consistently variable stem taxa that persist through time. Lineage segments are no less rigorously delineated than fossil species and have the same utility for drawing biostratigraphic and evolutionary conclusions. While lineage segments do not equal biological species, they represent the lowest-level taxonomic unit observable within *Hyopsodus* outside of the circumstances of absolute penecontemporaneous association. The pattern of *Hyopsodus* dental evolution is real. This pattern has been given the utmost consideration when compared to cladistic methodology and species relationship statements that either: (1) obscure this pattern by ignoring intermediates and variation, or (2) force more precise statements from this pattern than the data afford. The presence of a dense fossil record incorporating relative time is too valuable to ignore and the evolutionary pattern and relationships of *Hyopsodus* could not have been determined without the ability to track change through time.

Successive lineage segments are closely related to one another in an evolutionary sense, but would not always appear so on a cladogram. If a certain lineage segment gives rise to a derived form independently from another earlier or later lineage segment of the same species then, cladistically, the lineage as a whole is paraphyletic. While cladograms can suggest degree of relationship among discrete taxa, they do not describe patterns of evolution well within recognized lineage segments. With increasing documentation of anagenetic change, cladograms have less utility in describing phylogenetic pattern.

The theoretical decoupling of within-taxa anagenesis and speciation is crucial to understanding the phylogenetic pattern of *Hyopsodus.* Evolution, and therefore phylogeny, is a function of time, whereas cladistic analysis documents similarities and differences without regard to time. Neither stasis/punctuation nor gradual evolution can be accounted for in a cladogram. Both demand the analysis of temporal series.

Workers who have discovered similar evolutionary modes in fossil taxa have not agreed on systematic resolution (compare Krishtalka and Stucky [1985] to Bown and Rose [1987] to Martin [1995]). The systematics of *Hyopsodus* proposed here are meant to allow an easily changeable classification in that it makes as few species-level assertions as possible. Perhaps there is a need for consistent taxonomy and approach for instances of dense stratigraphic representation of taxa through time. A cladogram will shed no light on within-species change because its operational units must be discrete, negating the attempt to define continua.

The role of geographic variation is also problematic and should be considered. Geographic variants of *Hyopsodus* are not given taxonomic names in this study; certain key character frequencies seem to ally some of these variants. In the future, the taxonomic method used might also be applied geographically (not as true subspecies unless the evidence can be shown to meet all the biologic requisites) as well as temporally. Cenozoic temporal resolution, relative abundance of fossil taxa, and fossil species criteria are not now standardized to the point where this is possible.

Following the practice of Krishtalka and Stucky (1985), each lineage segment is represented by a diagnostic series rather than a single type specimen. Holotypes designated in the literature are indicated in both the referred specimens and the diagnostic series sections. A diagnostic series better represents the range of variation observed within lineage segments than a single type and avoids holotypic designations that obviously cannot reflect this variation.

The diagnoses have more meaning when considered as integrated character complexes; in most cases no one character state is diagnostic of all specimens in a lineage. Referred specimens are listed under lineage segments, when appropriate. In instances in which the material preserves no diagnostic features enabling confident classification, the referral is tentative and marked with a "?." Tentatively referred specimens show no morphology that conflicts with the systematic diagnosis of the taxon in question. In instances in which isolated teeth and jaw fragments of more than one species were erroneously catalogued under one CM number, these numbers are referenced in this study as containing discrete taxa "in part." To avoid any confusion, they are not assigned to the diagnostic series of any of the *Hyopsodus* lineages reported here.

Species and lineage-segment diagnoses are relatively long and, in the case of long-lived species, only partly comparative in syntax. This was chosen as the most accurate method of fully describing the nature of character expression and frequency of characters. One reason for doing this is that some dental evolution in *Hyopsodus* is of a mosaic type (see Barnosky, 1993). For example, while the length of P_4 is generally static and then decreases through time in the species *Hyopsodus paulus,* the relative length of the talonid appears to increase until a certain time (Lysitean) and then decreases in proportion to the overall shortening of the tooth. Since species change, but maintain their integrity, a diagnosis cannot fully describe the entire morphologic complex through time. The diagnoses, to a large extent, are entirely new and do not indicate the comparison of new material to a holotype or a diagnosis made on a limited number of specimens. Rather, they are based on comparison of the variability of one temporally constrained "population" to another. The illustrations show both salient diagnostic characters and variability. All were drawn from the same view under upper left side lighting. The specimens illustrated highlight the range of variability typical of the lineage segments.

Lineage-segment boundaries reported here correspond very closely to biostratigraphic boundaries. This is somewhat misleading. Although the terrestrial North American Eocene record is good, it is permeated by gaps that are reflected biologically as well as geologically. This does not mean that morphologic or systematic change occurs only at biostratigraphic or lithologic boundaries; segments are as easily broken into biostratigraphic boundaries as using unfamiliar boundary points.

Statistical and graphic meristic data appear in individually cited tables and figures; a listing of all measured specimens by locality is available in electronic format from the author. A key to frequently used dental terminology is given in Figure 2. The dentition of *Hyopsodus* is exceedingly well known and need not be further described here. A description of the general morphology of all upper and lower teeth is included in Gazin (1968). Type specimens important for comparison are illustrated in Figure 3.

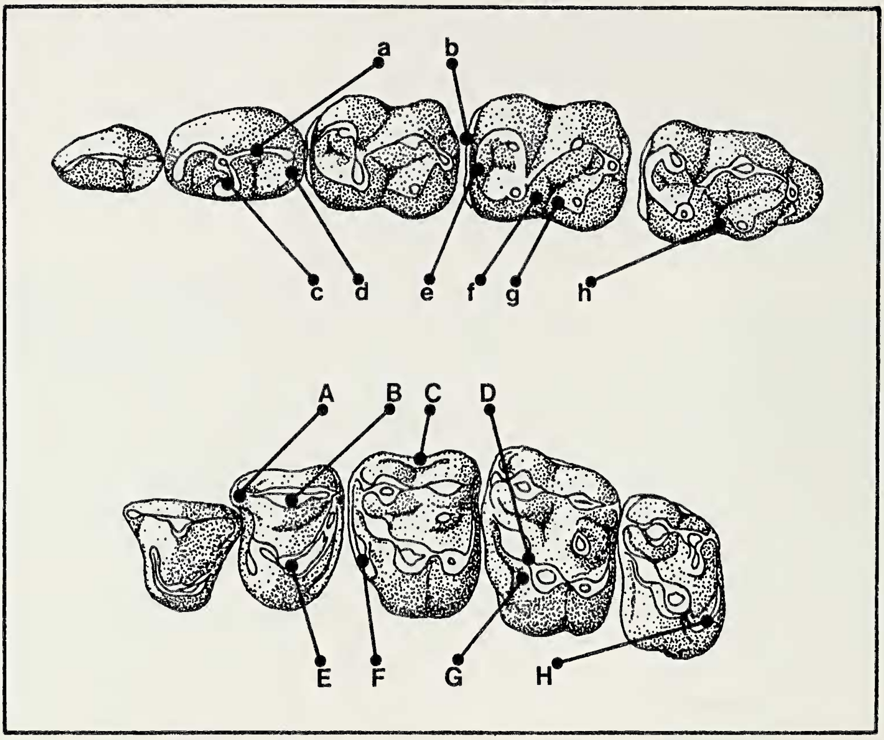

Fig. 2.—Key to *Hyopsodus* dental terminology. Unless designated, term refers to all teeth of a particular series. a, P_4 hypocristid; b, anterior cingulum; c, P_4 metaconid; d, position of P_4 metaconid; e, paralophid; f, position of molar metastylid; g, position of molar entostylid; h, talonid notch, molars and premolars; A, premolar parastyle; B, premolar paracone; C, ectocingula, labial cingula; D, molar protoloph; E, premolar protocone; F, anterior cingulum; G, anterior wall of trigon; H, hypocrista, position of hypocone.

SYSTEMATIC PALEONTOLOGY

Order Condylarthra Cope, 1881

Family Hyopsodontidae Lydekker, 1889

Hyopsodus Leidy, 1870

Stenacodon Marsh, 1872.
Lemuravus Marsh, 1875.

Type Species.—*Hyopsodus paulus* (Leidy, 1870).

Known Distribution.—Earliest to late middle Eocene of North America, Eocene of Europe and Asia.

Wasatchian and Early Bridgerian Species.—*Hyopsodus paulus, H. minusculus, H. minor, H. loomisi, H. powellianus, H.* sp., cf. *H. mentalis.*

Hyopsodus paulus Leidy, 1870
Microsyops vicarius Cope, 1873.
Hyopsodus vicarius Cope, 1875.
Esthonyx miticulus Cope, 1874.
Hyopsodus miticulus Cope, 1877.
Lemuravus distans Marsh, 1875.
Hyopsodus wortmani (type only) Osborn, 1902.

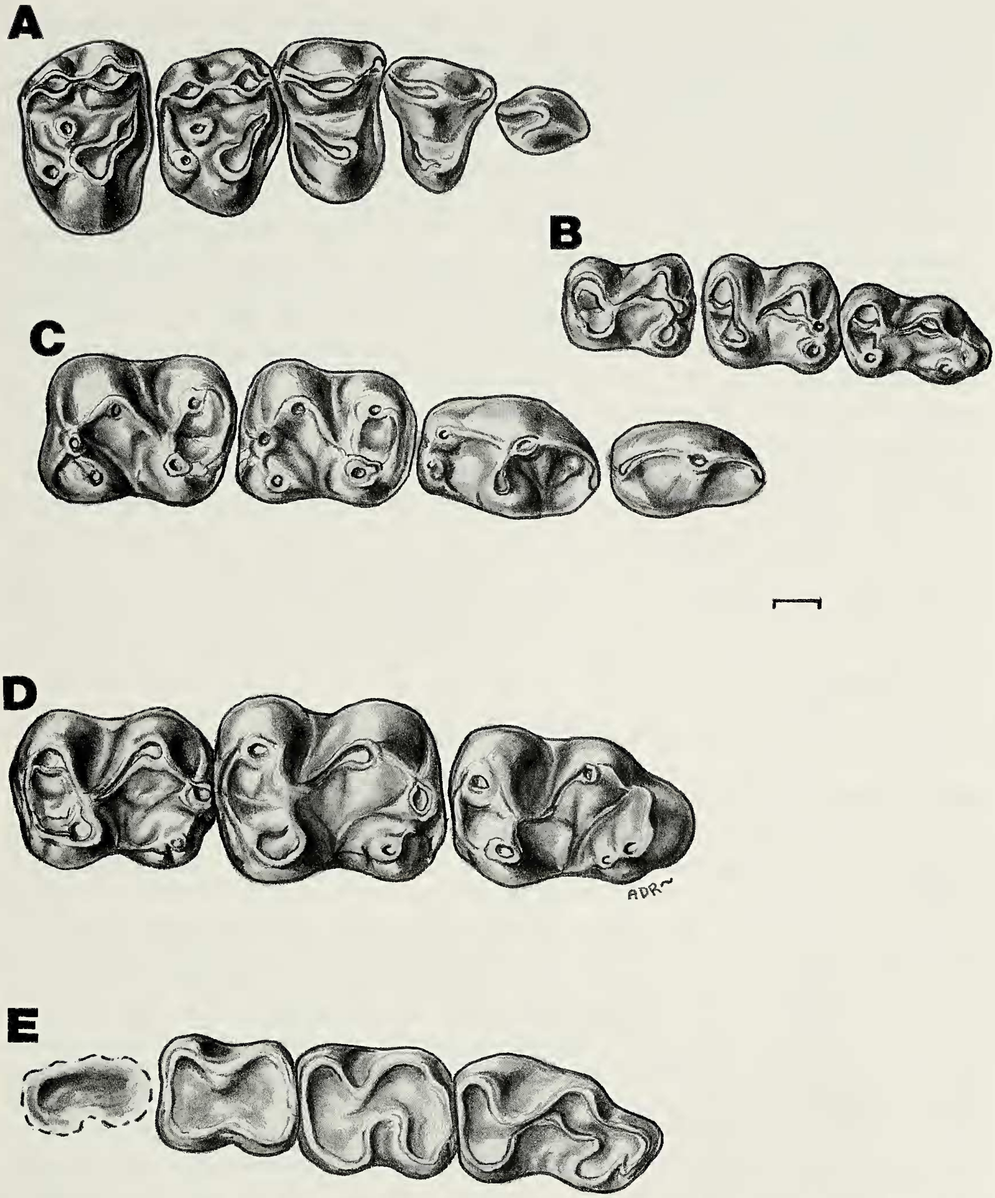

Fig. 3.—Type specimens of *Hyopsodus*. A, UCMP 44781, holotype of *Hyopsodus loomisi*; B, ACM 3492, holotype of *Hyopsodus minor*; C, AMNH 4139, holotype of *Hyopsodus lemoinianus*; D, AMNH 4147, holotype of *Hyopsodus powellianus*; E, USNM 1176, holotype of *Hyopsodus paulus*, type species of *Hyopsodus*. Scale equals 1 mm.

Hyopsodus marshi Osborn, 1902.
Hyopsodus simplex Loomis, 1905.
Hyopsodus despiciens Matthew, 1909.
Hyopsodus mentalis lysitensis Matthew, 1915*b*.
Hyopsodus latidens Denison, 1937.

Holotype.—USNM 1176, RP_4–M_3. Collected from Smith's Fork of Green River near Fort Bridger, Bridger Formation, Bridger Basin, Wyoming.

Included Lineage Segments.—Hyopsodus paulus–paulus, H. paulus–wortmani, H. paulus–lysitensis, H. paulus–simplex.

Diagnosis.—Length of second lower molar between 3.7 and 4.8 mm. Always smaller than *H. powellianus,* smaller than penecontemporaneous *Hyopsodus* sp., cf. *H. mentalis,* larger than *H. minusculus, H. minor,* slightly larger than *H. loomisi.* Differing from *H. powellianus,* P^3 transverse (labial–lingual) width greater than anterior–posterior length. Differing from *H. powellianus* and *H. loomisi,* parastyle on P^3 and P^4 smaller, but more distinct than *H. minor.* M^3 occlusal outline more nearly square than other *Hyopsodus* due to a well-developed, somewhat posteriorly situated metacone. M^3 hypocone comparatively better developed than *H. loomisi,* featuring larger basal area where the cusp is confluent with the hypocrista. Upper molar paraconules more robust at base (somewhat crescentic in later lineage segments) where they join the protoloph that runs anterolabially to the junction of the paracone base and anterior cingulum. Anterior cingula and ectocingula of upper molars broader and more deeply excavated than penecontemporaneous lineages of similar or smaller size. Unlike *H. minor* or *H. powellianus,* P_4 talonid with variably developed entoconid. Differing from *H. loomisi,* width of the talonid greater than width of the trigonid on M_{1-2}. Paralophid (anterior cristid of trigonid) inflected slightly anterolingually (more than *H. loomisi, H. minor*; less than *H. powellianus*) before ascending to meet the metaconid.

Referred Specimens.—Listed under individual lineage segments.

Known Distribution.—Earliest Wasatchian through middle Bridgerian (Sandcouleean through Blacksforkian) of western North America.

Discussion.—Some of the above-listed characters are shared with larger-sized lineages of *Hyopsodus* and *Hyopsodus minusculus* (indicative of relationship at different levels), but are developed to differing degrees and are associated as parts of discrete character complexes. Temporally adjacent lineage segments of *Hyopsodus paulus* show considerable overlap in frequency and degree of character expression, but because the canalized traits of lineages result in observable morphoclines, the earliest lineage segments do not overlap with the youngest lineage segments. For example, *Hyopsodus paulus–paulus* is quite distinct from *Hyopsodus paulus–simplex,* whereas *Hyopsodus paulus–lysitensis* includes specimens that are not as distinct from the latter. Given the apparent evolutionary rate and mode in *Hyopsodus* (substantiated by change in size of M_1 by Gingerich, 1974*a*), this phenomenon accurately reflects the true phylogenetic relationships of taxa with an extremely dense fossil record (see Krishtalka and Stucky, 1985: 479).

In this report, the taxon *Hyopsodus paulus* encompasses most specimens assigned to *Hyopsodus miticulus* (as conceived by Gazin, 1968), some specimens of *Hyopsodus mentalis* (Cope, 1875), the holotype of *Hyopsodus simplex* (Loomis, 1905), and *Hyopsodus latidens* (Denison, 1937). In the Wind River Basin, *H. paulus* includes Lysite and Lost Cabin Member individuals referred to *H. miticulus* by Guthrie (1967, 1971), as well as Stucky's (1982) *H. paulus* from the uppermost Lost Cabin Member. The latter specimens show no derived characters that distinguish them from the type or referred Bridgerian specimens of *H. paulus* and are only slightly more primitive than Blacksforkian *Hyopsodus paulus* in degree of character development.

The species *Hyopsodus paulus* here also includes the type of *Hyopsodus wortmani* (Osborn, 1902). *Hyopsodus wortmani* has long been accepted as a valid species of small *Hyopsodus* from the Wind River Basin, but examination of the holotype (AMNH 4716) has shown that it falls within the range of morphologic and size variability of the Lostcabinian lineage of *Hyopsodus paulus*. Characters of the type specimen supporting this conclusion include the presence of an entoconid on P_4, a transversely wide M_2, and the structure of the hypocone on M^3. The locality information and preservation of this specimen suggest that it was probably collected from the type area of the Lost Cabin Member, which is a Lostcabinian locality. This taxonomic decision is discussed in more detail below. Many other specimens of "*H. wortmani*" collected from the American Museum's Davis Ranch locality (= CM loc. 34) are referred here to *Hyopsodus minusculus*.

Anagenetic character acquisitions in *Hyopsodus paulus*, from Sandcouleean through middle Bridgerian, include: (1) increase in size of upper and lower third molars, increasingly well-developed hypocone on M^3, more distinct entoconid and hypoconulid on M_3 (also noted by Matthew, 1915*b*); (2) more widely spaced bases of hypocone and protocone on M^1 and M^2; (3) labiolingual compression of P^4 paracone; (4) increasingly distinct upper premolar and molar external cingula, particularly the ectocingula; (5) better developed and more distinct external ribs on the upper molar paracone and metacone and the P^3 and P^4 paracones; (6) decreasing robusticity of cusps and increasing lophodonty of upper and lower premolars and molars; (7) increasing height of lower premolar hypocristid and talonid notching of lower premolars and molars; (8) anterior shifting of molar protoconid and hypoconid, lingual shifting of hypoconulid; (9) decreasing anteroposterior length of P_3 and P_4 relative to lower molar length.

Hyopsodus paulus is the most common species of *Hyopsodus* in the Wind River Basin, and also appears to be extremely well represented in the Wasatchian of the Bighorn and Green River basins (following the analyses of Gazin, 1968, and Gingerich, 1974*a*). Among the localities examined here, its presence is indicated (histograms cited under lineage segments) by specimens clustering about a mean lower second molar length of approximately 4.2 mm during the Graybullian through Lostcabinian, and 4.5 mm in the Gardnerbuttean (Table 3). By Blacksforkian time, *H. paulus* was the most common species of *Hyopsodus* (West, 1979*a*) and is the most abundant faunal element at most localities (Gazin, 1968). It co-occurs with *Hyopsodus loomisi* at Sandcouleean through ?mid-Graybullian localities, *Hyopsodus minor* in the late Graybullian through Lysitean (possibly earliest Lostcabinian), lineage segments of *Hyopsodus powellianus* in the Lysitean through Gardnerbuttean, and *Hyopsodus minusculus* in the earliest through middle Bridgerian.

The principles of classification utilized in this study imply, artificially by some workers' standards, that *Hyopsodus paulus* was a very long-lived "species" that was present in the earliest Wasatchian. It seems to possess more advanced characters when compared to the lithosympatric *Hyopsodus loomisi* at the Sandcouleean Four Mile locality (McKenna, 1960). Gingerich (1974*a*) gives evidence for only one small *Hyopsodus* form in the basal Willwood; however, both McKenna (1960) and Bown (1979) document two *Hyopsodus* phena at least this early. The earliest record of *Hyopsodus*, from the Clarkforkian (Rose, 1981), is still very poor. Thus, it cannot be confidently stated whether *Hyopsodus paulus* or *H. loomisi* more closely approximates the primitive condition for *Hyopsodus*,

Table 3.—Summary of statistics, lower dentitions of *Hyopsodus paulus* (lineage segments *H. paulus–paulus, H. paulus–wortmani, H. paulus–lysitensis, H. paulus–simplex*). High, low, mean, SD in mm.

	P_3 (L, W)	P_4 (L, W)	M_1 (L, W)	M_2 (L, W)	M_3 (L, W)
H. paulus–paulus					
High	3.4, 2.3	4.0, 2.9	4.6, 4.0	4.8, 4.3	5.5, 3.8
Low	3.0, 2.0	3.3, 2.3	3.9, 3.1	4.2, 3.5	4.5, 3.1
n	10	46	76	114	88
Mean	3.1, 2.2	3.6, 2.6	4.3, 3.6	4.5, 3.9	5.0, 3.5
SD	0.12, 0.09	0.15, 0.14	0.17, 0.17	0.15, 0.18	0.21, 0.14
CV	3.9, 4.1	4.2, 5.4	4.0, 4.7	3.3, 4.6	4.2, 4.0
H. paulus–wortmani					
High	3.4, 2.4	3.9, 2.9	4.3, 3.6	4.6, 3.8	5.1, 3.5
Low	2.6, 1.9	3.0, 2.2	3.6, 2.8	3.8, 3.2	4.1, 2.8
n	17	48	76	88	66
Mean	3.0, 2.1	3.5, 2.5	3.9, 3.1	4.2, 3.5	4.6, 3.1
SD	0.19, 0.14	0.15, 0.14	0.16, 0.16	0.20, 0.13	0.22, 0.14
CV	6.3, 6.6	4.3, 5.6	4.1, 5.2	4.8, 3.7	4.8, 4.5
H. paulus–lysitensis					
High	3.5, 2.5	3.9, 3.0	4.5, 3.8	4.6, 4.0	4.9, 3.7
Low	3.0, 1.8	3.3, 2.4	3.6, 2.9	3.8, 3.2	3.9, 2.7
n	14	51	105	161	124
Mean	3.2, 2.2	3.5, 2.6	3.9, 3.2	4.2, 3.5	4.5, 3.1
SD	0.18, 0.18	0.14, 0.14	0.16, 0.16	0.15, 0.15	0.18, 0.17
CV	5.6, 8.2	4.0, 5.4	4.1, 5.0	3.6, 4.3	4.0, 5.5
H. paulus–simplex					
High	3.3, 2.4	3.7, 2.8	4.1, 3.5	4.4, 3.9	5.0, 3.5
Low	3.0, 2.0	3.2, 2.3	3.4, 2.6	3.6, 3.2	3.7, 2.7
n	11	35	47	79	60
Mean	3.1, 2.1	3.5, 2.6	3.7, 3.1	4.1, 3.6	4.2, 3.1
SD	0.12, 0.13	0.11, 0.10	0.14, 0.17	0.16, 0.14	0.22, 0.13
CV	3.9, 6.2	3.1, 3.8	3.8, 5.5	3.9, 3.9	5.2, 4.2

or which of these species occurs first in the North American fossil record.

Lineage Segment *Hyopsodus paulus–paulus*
(Fig. 4, 5; Tables 3, 4)

Diagnosis.—Largest (mean length of M_2) lineage segment of *Hyopsodus paulus.* Taller, more gracile cusps than pre-Bridgerian *H. paulus*; also generally more lophodont molars. M^2 paraconule more robust and crescentic in occlusal view than in *H. minusculus.* M^3 more rectangular with more distinct hypocone than in *H. minusculus.* Most distinct parastyle within *Hyopsodus paulus.* In contrast to earlier lineage segments, lower molar trigonid more elevated; paraconid almost universally absent. In contrast to *H. powellianus–walcottianus,* molar entostylids infrequent and not inflated. Entoconid and hypoconulid more lingually shifted than other Wasatchian or early Bridgerian *Hyopsodus,* consequent arcuate hypoconid with long posthypocristid.

Diagnostic Series.—USNM 1176 (type, *Hyopsodus paulus*). CM 21089, 21092, 22321, 30932, 35734, 40083, 44957, 44969, 55225. UCM 46599. ANSP 10253, 10256.

Referred Specimens. CM 4953, 21044 (in part), 21046, 21048, 21051, 21054, 21056, 21059–21060,

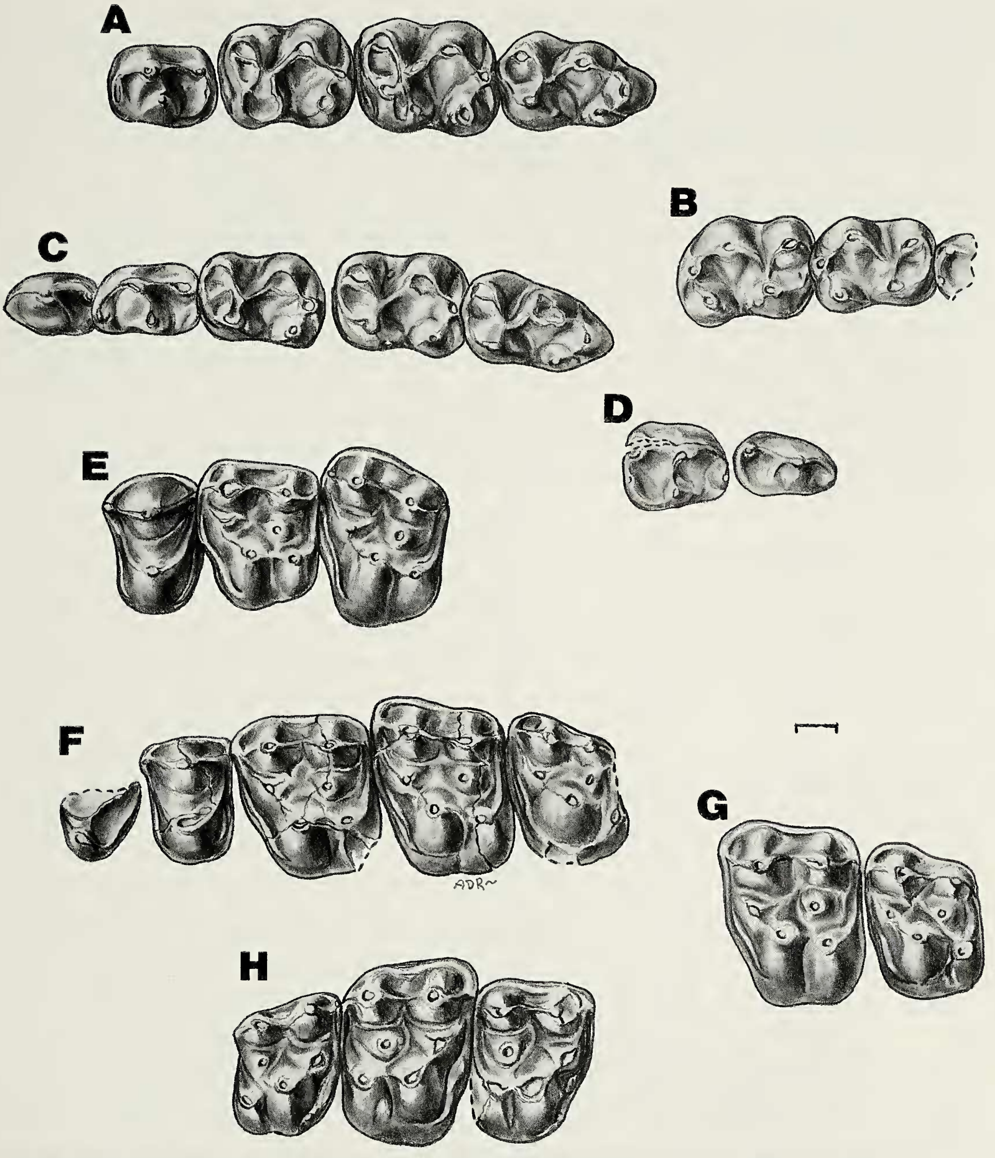

Fig. 4.—Specimens of *Hyopsodus paulus–paulus.* A, CM 36449; B, CM 35722; C, CM 40083; D, CM 36447; E, CM 21092; F, CM 22588; G, CM 55258; H, CM 29126. Scale equals 1 mm.

21062, 21065–21070, 21076, 21078, 21081, 21083–21085, 21088, 21090, 21092, 21095–21096, ?21097, 21101, 21103, 21105, 21107–21108, 21921–21922, 22314–22318, 22320–22323, 22531 (in part), 22588, 27439, 27447–27448, 29125–29126, 29130, 29133, 29135 (in part), 30887–30889, 30895, 30898, 30900, 30903–30904, 30906, 30909, 30916–30917, 30919–30920, 30925–30927, 30930–30932, 30935–30937, 31001, 31004, 31007–31008, 31013–31014, 35721–35731, 35733–35740, ?35741, 35743, 35745, 35747–35752, ?35753, 35754–35757, 35760, 36447 (in part), 36449, 36930, 36941, 36945, 37331 (in part), 37332 (in part), 40081–40083, 40085–40088, 40092, 40094, 40098–40099, 40614–40615, 40617, 40619–40625, 40629–40630, 40633, 40636, 40640, 40645, 40650, 40653, 40655, 40657, 40659, 40661–40662, 40674–40675, 40677, 40752, 44914–44915, 44917–44918, 44923 (in part), 44931–44937, 44940, 44944, 44946, 44955, 44956 (in part), 44957–

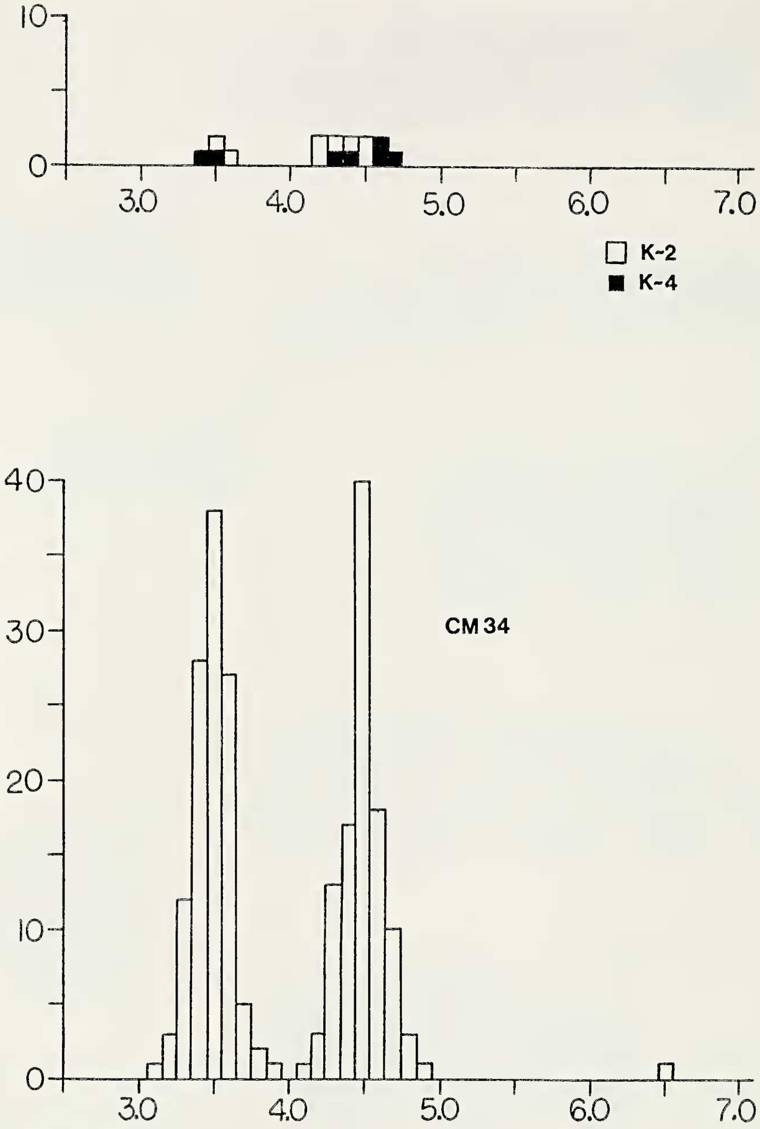

Fig. 5.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Gardnerbuttean localities. Vertical axis, number of individuals; horizontal axis, molar length in mm.

44958, 44960, 44963–44965, 44967–44970, 44972–44973, 44974 (in part), ?44980, 44981, 44984–44990, 44993–44998, 45163, 45185, 45191–45193, 45284–45285, 45321, 45330, 45959, 45963–45964, 45968–45970, 45972, 45978, 46657, ?47227, 55032, ?55033, 55034, 55036–55038, 55040–55047, 55049, 55051, 55053, 55057, 55059–55060, 55063–55064, 55067–55070, 55072, 55074, 55076–55077, 55079, 55082–55083, 55221–55222, 55225, 55227–55229, 55233–55234, 55238, 55240–55241, 55246, ?55248, 55249–55252, 55255–55256, 55258–55260, 55268–55270, 55272, 55274, 55276–55279, 55283–55285, 55289, 55292–55293, 55295–55297, 55299, 55300–55301, 55304, 55307–55311, 55314, 55316–55317, 55319, 55322, 55324, 55326, 55329. UCM 44831, 44861, 45298, 45300, 45303, 45365–45366, 45430, 46473, 46549, 46586–46589, 46592, 46599. UW 23517, 23527. ANSP 10252–10253, 10255–10256, 10258. USNM 1176 (type, *H. paulus*).

Localities.—CM 34 (Davis Ranch of AMNH), 1036, 1038, 1543, 1545, 1548. UCM 80064, 80065, 81026. UW V89041. ANSP Grizzly Buttes locality (Blacksforkian).

Known Distribution.—Earliest Bridgerian (Gardnerbuttean) of Wind River Basin, Wyoming, and Huerfano Basin, Colorado; Blacksforkian of western North America.

Discussion.—The diagnostic characters described above are best developed in Blacksforkian specimens; Gardnerbuttean specimens are less lophodont overall and somewhat less progressive in the degree of lower premolar shortening and the anterior placement of the molar protoconid and hypoconid. Gardnerbuttean specimens are allocated to *H. paulus–paulus* because they most closely approach Blacksforkian specimens in character acquisition, even though they are often less well developed. As in the Blacksforkian, they are associated with a lithosympatric small *Hyopsodus* lineage. Segment name *paulus* indicates the affinities of Gardnerbuttean specimens to Blacksforkian *Hyopsodus paulus,* but Wind River specimens are overall more primitive in morphology. On the other hand, they are very close to later Bridgerian specimens in size.

In the Wind River Basin, a large sample of *Hyopsodus paulus–paulus* has been recovered from CM loc. 34. At this locality, *H. paulus–paulus* shows a normal distribution of size and character development with virtually no overlap with the smaller, lithosympatric, and penecontemporaneous *H. minusculus.* The smallest specimens of *H. paulus–paulus* and the largest *H. minusculus* approach each other in size (there is no overlap at CM loc. 34) but are distinct in premolar structure and the shape and proportions of the molars.

Hyopsodus paulus appears to be stable in molar size throughout the middle Bridgerian (West, 1979*a,* 1979*b*). Although Gardnerbuttean *Hyopsodus paulus* is somewhat more primitive than the type specimen and other Bridger B material examined (e.g., ANSP 10252–10253, 10255–10256, 10258), the majority of specimens possesses all of the diagnostic characters listed above and is similar in size. Dentitions of *H. paulus* from the ANSP Grizzly Buttes locality have taller, more gracile cusps (especially the metaconid), and more lingually shifted and closely placed molar entoconids/hypoconids. The lower premolar series is also shorter. Gazin (1968:16) noted that in Bridgerian *Hyopsodus,* P^2 is occasionally single rooted, a condition not confirmed in the earliest Bridgerian CM sample.

Hyopsodus paulus–paulus is the final segment of the *Hyopsodus paulus* evolutionary lineage within the Wind River Basin. The work of West (1979*a,* 1979*b*) and Krishtalka (1979) indicates that the "species" continues through the Bridgerian into the Uintan. AMNH and ANSP material, as well as CM specimens from the Powder Wash locality of the Green River Basin, show increasing canalization of the traits which first distinguish *H. paulus–paulus* in the earliest Bridgerian. Analysis of later Bridgerian material could well indicate that additional segments of *Hyopsodus paulus* should be recognized and that Gardnerbuttean specimens should relinquish their claim on segment name *paulus.*

Morphologically, *H. paulus–paulus* does overlap with individual specimens of Lostcabinian *Hyopsodus paulus–wortmani,* but *H. paulus–wortmani* is smaller on average, does not uniformly feature a P_4 with a distinct paraconid and a well-developed posthypocristid with an entoconid, and is less lophodont overall. Only a few specimens of *H. paulus–wortmani* are as derived as *Hyopsodus paulus–paulus* in the expression of upper dental characters. Lostcabinian *H. paulus* shares anagenetic characters with *Hyopsodus paulus–paulus,* but only in comparison to earlier lineage segments of the same species.

At localities where large collections have been made (e.g., CM loc. 34 and CM loc. 1046), *Hyopsodus paulus–paulus* occurs in lithosympatry with *H. minusculus* and the much larger *Hyopsodus powellianus–walcottianus* (Fig. 5), whereas *H. paulus–wortmani* occurs only with *H. powellianus–walcottianus* (see Fig. 7). Importantly, *Hyopsodus paulus–wortmani* shows a normal distribution of dental features later canalized differently by *H. paulus–paulus* and *H. minusculus. Hyopsodus paulus–paulus* shares more lophodont molars, especially the hypoconid, shorter P_{3-4}, long M_3, well-developed ribs on the upper dentition, and stronger molar hypocones and anterior and labial cingula with *Hyopsodus minusculus.* This suggests that both Bridgerian forms are descended from a single Lostcabinian lineage. Robinson's (1966) quantitative data for Huerfano *Hyopsodus* can also be interpreted as indicative of a single, intermediate-sized Lostcabinian species and two discrete (somewhat larger and smaller) Gardnerbuttean lineages.

Robinson (1966), and later, Stucky (1982), applied *Hyopsodus paulus* to Lost Cabin Member specimens in the Wind River Basin; Gazin (1968) and Guthrie (1971) preferred the name *Hyopsodus miticulus* (Cope, 1874, 1877), which was originally based on material from the San Jose Formation. The holotype of *Hyopsodus miticulus* is lost, and the species lacks a diagnosis, making this nomen inappropriate for material from the Wind River Basin.

Gazin's review (1968), based solely on the length of M_2, indicates that intermediate and small *Hyopsodus* lineages co-occur in the Lostcabinian "Knight Member" equivalents of the Green River and Washakie basins. The stratigraphic resolution of these collections is poorly refined, but if Gazin's conclusions are correct, the co-occurrence of *Hyopsodus paulus–paulus* and *Hyopsodus minusculus* may be typical only of earliest Bridgerian sediments in the Wind River and Huerfano basins. However, earlier work by Gazin (1962) indicated a small form of *Hyopsodus* was common only in the New Fork Tongue, higher stratigraphically than the first occurrence of the "species" *H. walcottianus.* As will be discussed below, "*H walcottianus*" is most common in Lostcabinian rocks; therefore, New Fork Tongue strata may be younger.

Lineage Segment *Hyopsodus paulus–wortmani*
(Fig. 6–8; Tables 3, 4)

Diagnosis.—Smaller in mean size than *Hyopsodus paulus–paulus.* Intermediate between lineage segments *H. paulus–paulus* and *H. paulus–lysitensis* in degree of lophodonty and gracility of all teeth. Features more frequently and strongly developed than in *H. paulus–lysitensis* include: external cingula on upper premolars and molars; height and compression of premolar paracone and molar paracone and metacone; taller, more gracile molar protocone with less robust base; more distinct ribs on external cusp margins of upper dentition; open molar talonids, entoconid less robust with less frequently developed entostylid; molar trigonid taller with less tendency to exhibit paraconid. Compared to lineage segment *H. paulus–paulus, Hyopsodus paulus–wortmani* is less lophodont overall; smaller in mean size; does not uniformly show the diagnostic lower premolar morphology and more rarely exhibits hypoconulid reduction and lingual shifting of posterior talonid cusps on M_{1-2}.

Diagnostic Series.—AMNH 4716 (type, *Hyopsodus wortmani*), 14611. CM

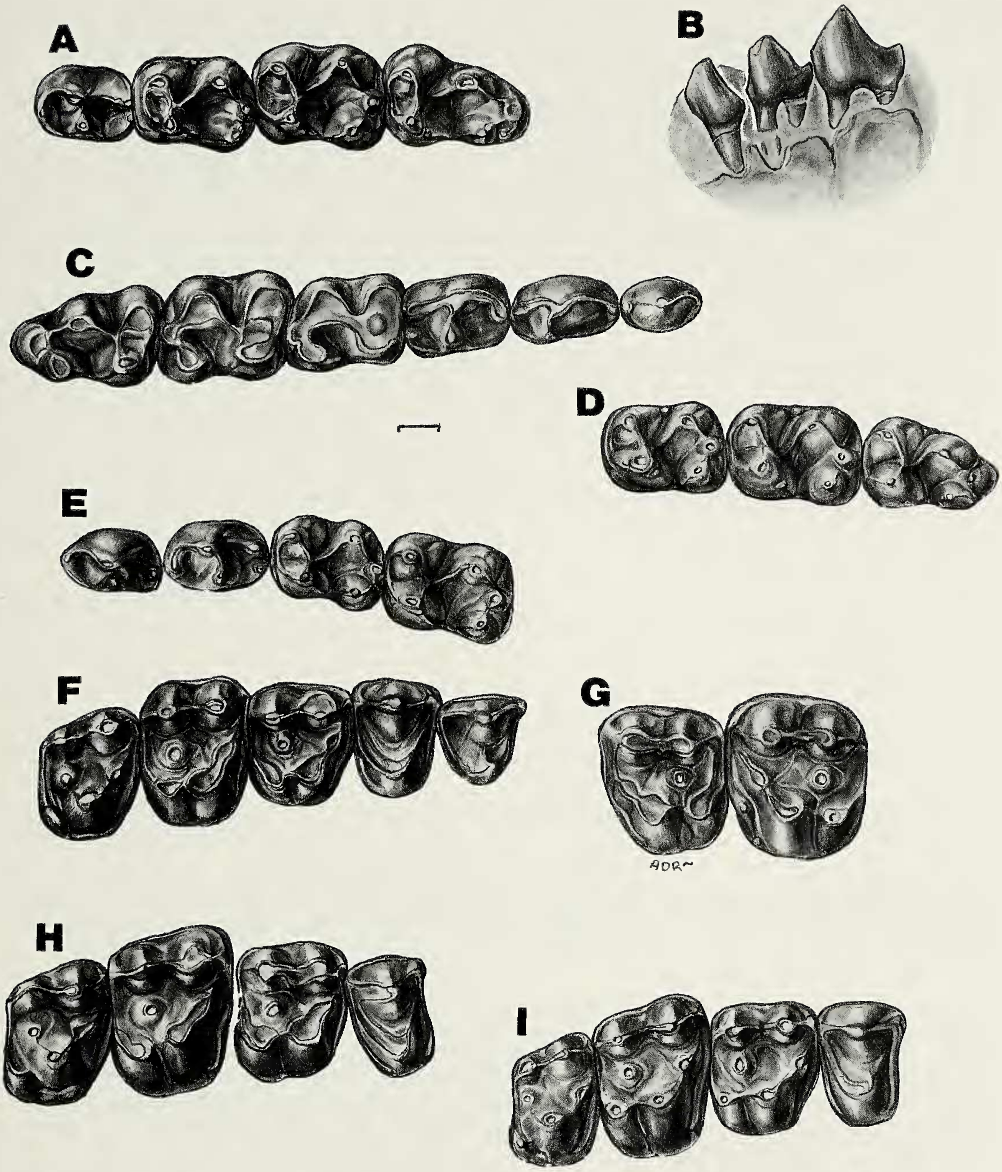

Fig. 6.—Specimens of *Hyopsodus paulus–wortmani.* A, CM 60560; B, CM 60561; C, CM 45233; D, CM 49459; E, CM 45244; F, CM 46647; G, CM 45133; H, CM 45286; I, CM 49458. Scale equals 1 mm.

45152, 45202, 45223, 45244, 45259, 45286, 46647, 47171, 49458, 49460, 60560, 60561.

Referred Specimens.—CM 4959, 21214–21215, 21220 (in part), 22324–22327, 22329–22336, 22338, 22342, 34886, 36452–36455, 37226, 40665–40666, 40669–40672, 40679–40690, 44999, 45151–45152, 45154, 45156–45157, 45200–45231, 45233–45234, 45236–45256, 45258, 45260–45262, 45264–45266, 45268, 45270–45283, 45289, 45291–45295, 45299, 45300–45302, 45304, 45325–45327, 45329, 45932, 45961, 45998, 46644–46645, 46647, 47029, 47040, 47060–47061,

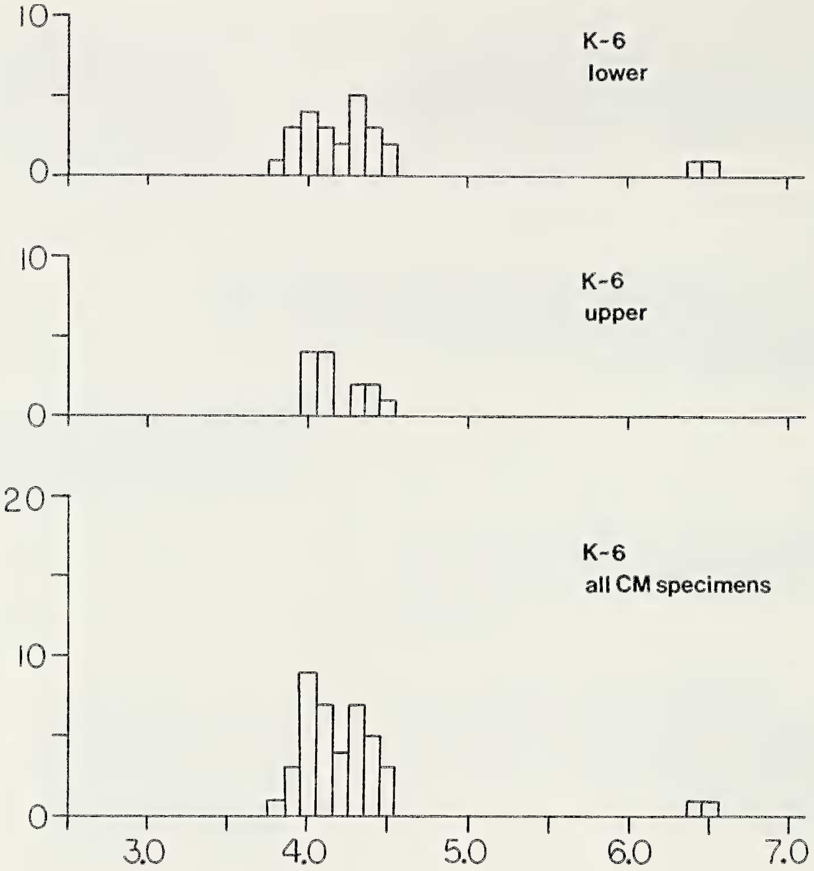

Fig. 7.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Lostcabinian locality 1040 ("K-6"). Vertical axis, number of individuals; horizontal axis, molar length in mm.

47080–47081, 47102, 47150–47152, 47166–47170, 49440–49444, 49446, 49449–49450, 49452–49457, 49459–49462, 49464–49465, 49477, 60560–60562. UCM 44328–44329, 44332–44333, ?44377, ?44393, 44394, 44414–44415, 44453–44454, 44560–44561, 45334, 45342, 45392, 46352, 46623, 46642–46644, 46797, 46799, 46800–46805, 46935–46937, 46965. AMNH 4716 (type, *H. wortmani*), 14611, 14633. ACM 10091. (Wind River, ?Lysite/?Lost Cabin) CM 34885 (in part), 37333, 40678, 40691, ?45935, 47127, 47129.

Localities.—CM 88, 90–91, 99, 856–857, 936, 1011, 1039, 1040–1043, 1046–1048, 1076–1078, 1080, 1534, 1541–1542, 1550–1551, 1908, 1910, 1952, 1959, Kay's loc. S.E. of Riverton. UCM 79043, 80088. AMNH Buck Springs loc. ACM type Lost Cabin loc.

Known Distribution.—?Late Lysitean and Lostcabinian of Wind River Basin, Wyoming; Lostcabinian of Huerfano Basin, Colorado; late Wasatchian of Bighorn and Green River basins, Wyoming.

Discussion.—The Lostcabinian lineage segment *Hyopsodus paulus–wortmani* provides the best documented illustration of the species-lineage evolutionary pattern in early Eocene *Hyopsodus*. This is due, in part, to the good stratigraphic resolution of the Lost Cabin Member in the Wind River Basin. The absolute

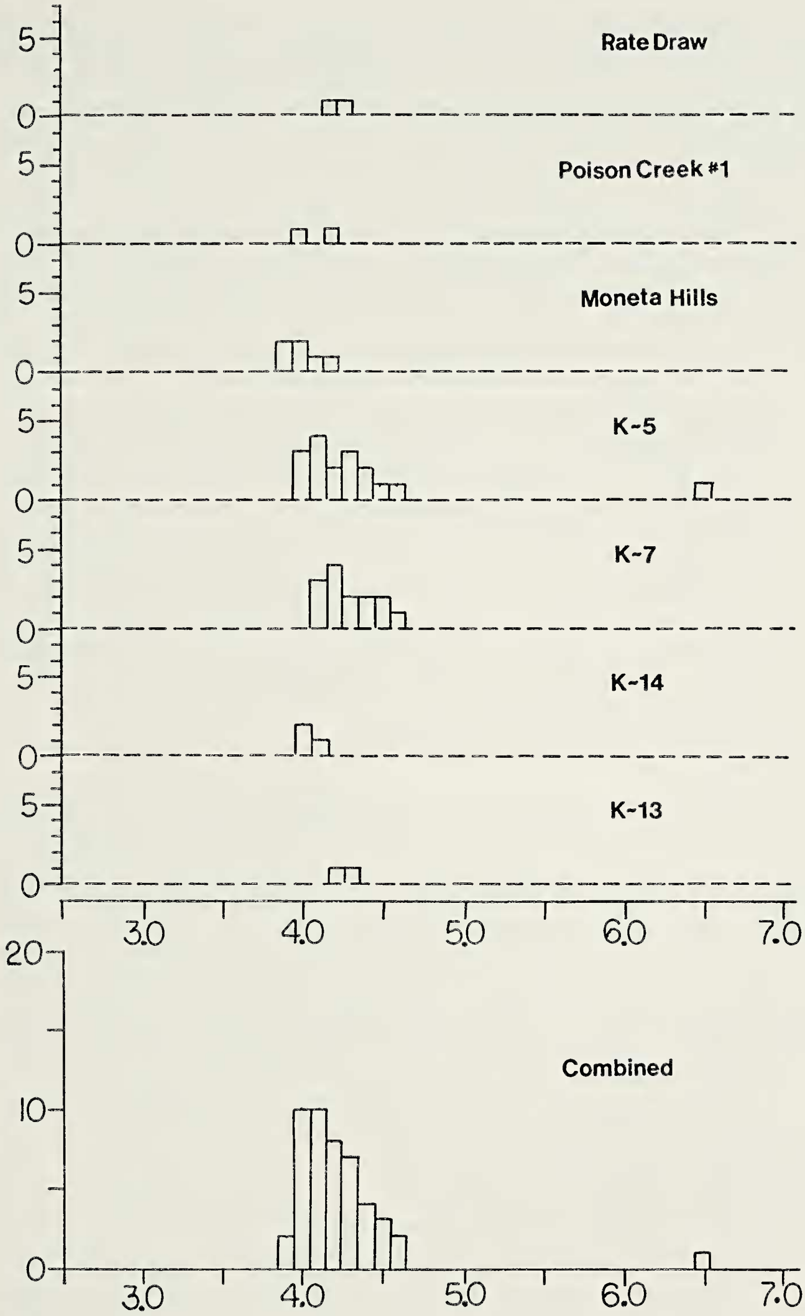

Fig. 8.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Lostcabinian localities, all data combined on lowermost histogram. Vertical axis, number of individuals; horizontal axis, molar length in mm.

variation in dental morphology is somewhat greater than in Gardnerbuttean *Hyopsodus* (this may be partly explained by the more geographically widespread Lostcabinian localities), but is no greater than Lysitean or Graybullian *H. paulus* or Lysitean *H. powellianus.* An insufficient number of middle Bridgerian *H. paulus* was examined for a confident assessment of character variability; the size of M_1 is quite stable (West, 1979*a*; 1979*b*).

In the middle to late Lostcabinian, specific characters that are normally distributed in a single lineage segment (*H. paulus–wortmani*) are later canalized differentially in two coexisting lineages by the early Bridgerian. The consistently varying characters of interest in *H. paulus–wortmani,* also noted to a similar degree in *H. paulus–lysitensis* (see below), are the length of P_3 and P_4, the development of the hypocristid and entoconid on P_4, strength and location of P_{3-4} paraconid, architecture of the hypoconulid and entoconid on M_1 and M_2, degree of expression of M^3 hypocrista, development of the upper molar protoloph and associated paraconule, and the length/width proportions of the upper molars. Histograms of the length of M_2 (Fig. 7, 8) indicate a slightly bimodal size distribution at some Lostcabinian localities, but characters are expressed evenly among the specimens examined. For example, CM 45233, a larger individual, features molar proportions and an open P_4 talonid similar to *H. minusculus* on the one hand, and a P_4 entoconid and overall size closer to *H. paulus–paulus* on the other. CM 45218 is located on the small end of the size frequency distribution (more similar to *H. minusculus*), but M_1 is wide with a well-separated hypoconulid/entoconid as in *H. paulus–paulus.* Significantly, the range of variation is not associated with size, regardless of the taxonomic status of the Lostcabinian sample (two versus one "species") or its resolution. This condition meets the criterion of a single lineage segment in this study.

Hyopsodus paulus–wortmani occurs commonly at middle to late Lostcabinian localities such as CM locs. 1040, 91, and 1046–1047, and also appears to occur at early Lostcabinian CM loc. 1550, the ?early Lostcabinian Okie Trail localities, and CM loc. 1952 (see histograms, Fig. 22). However, too few specimens are, as yet, available from these localities to refer them with certainty to *H. paulus–wortmani* (rather than *H. paulus–lysitensis*). As discussed below, at the Okie Trail and CM loc. 1952, the specimens in question are associated with larger and somewhat atypical *Hyopsodus* not found in the typical Lostcabinian fauna. The "*wortmani*-morphs" from the Okie Trail are listed with *H. paulus–wortmani* for the present time in order to form a testable hypothesis when more material is discovered. *Hyopsodus paulus–wortmani* is easily distinguished from the much larger and more bunodont *Hyopsodus powellianus–walcottianus* with which it is lithosympatric in the Lostcabinian.

The markedly bimodal size distribution of small and intermediate-sized *Hyopsodus* previously noted in the Lostcabinian of the Wind River Formation (see Lost Cabin frequency histogram in Gazin, 1968) is the result of mixing all collected specimens from the Lost Cabin Member, traditionally thought to represent one Land Mammal Subage. Because a large number of Lost Cabin Member *Hyopsodus* specimens are Gardnerbuttean in age, a Gardnerbuttean size distribution was strongly imprinted on the collective Lost Cabin Member data.

Gazin (1968) noted more elongate, basined fourth lower premolars in specimens of late Wasatchian "Knight Formation" *Hyopsodus.* No such trend is observable in the Lostcabinian of the Wind River Formation, although this character is common in Lysitean *H. paulus.*

There is no morphology in *H. paulus–wortmani* to support Gingerich's (1974*a*) derivation of Lostcabinian intermediate-sized *Hyopsodus* from the large-sized Lysitean lineage *Hyopsodus powellianus.*

Lostcabinian *Hyopsodus* is referred to *Hyopsodus paulus* rather than *Hyopsodus minusculus* (see below) because its size is slightly closer to early Bridgerian *H. paulus* and because its upper molars are more frequently closer to *Hyopsodus paulus* in the morphology of the protoloph and M^3 hypocone. Lower dentitions, both molars and premolars, are with almost equal frequency close in morphology to either *H. paulus–paulus* or *H. minusculus* from the Gardnerbuttean levels of the Lost Cabin Member of the Wind River Formation.

Lineage Segment *Hyopsodus paulus–lysitensis*

(Fig. 9–11; Tables 3, 4)

Diagnosis.—P_{3-4} posthypocristid stronger than *in H. paulus–simplex*; differing from *H. paulus–wortmani,* commonly wraps around talonid and runs anteriorly to the base of the metaconid; P_4 more nearly square than in *H. paulus–wortmani,* P_4 talonid less square than in *H. powellianus.* Compared to *H. paulus–paulus,* lower molars bunodont; entoconid and metaconid lower crowned; molar talonids relatively closed and not deeply notched as in *H. paulus–wortmani* and *H. minusculus*; paraconid more frequently developed on paralophid of M_1. Entostylid common, metastylid variably present and more common than in *H. powellianus.* M_3 hypoconulid lobe often imperfectly separate from entoconid. P^4 parastyle more anteriorly placed relative to paracone than in later lineage segments. M^{1-3} protoloph not as well developed, less crest-like, and with smaller paraconule than in *H. paulus–wortmani*; hypocone less elevated and somewhat more labially placed on M^{1-2} in majority of specimens.

Diagnostic Series.—AMNH 15621 (type, *Hyopsodus lysitensis*). CM 22703, 39162, 39169, 39172, 39752, 39803, 46841, 49421, 54106. ACM 11078.

Referred Specimens.–(Wind River, Lysite) CM 19811, 19818, 19823, 19825, 19827, 19829–19831, 19836–19837, 19839, 19850, 19851 (in part), 19852 (in part), 19853, 20878–20879, 20920–20925, 20939–20940, 20942, 21789–21790, 21898, 21901–21904, 21907, 21909–21910, 22680, 22687, 22694, 22701–22702, 22710 (in part), 22718 (in part), 22735 (in part), 22736 (in part), 28652–28655, 28657–28663, 28665, 28667 (in part), 28668 (in part), 28669, 28724, 28731, 28733, 28756, 28759, 28760 (in part), 28761 (in part), 28762 (in part), 28764, 28766, 28770, 28774 (in part), 28777, 28778 (in part), 28936 (in part), 28937, 29191–29195, 29196 (in part), 31349–31351, 35891, 35896, 35905, 35909, ?35910, 36071, 36072 (in part), 39148, 39158, 39164, 39169, 39171–39172, 39176, 39178, 39181–39183, 39186–39187, 39190, 39192, 39204, 39217, 39231, 39233, 39235, 39237–39238, 39240, 39244–39245, 39279, 39286, 39290–39291, 39293–39295, 39518, 39550, 39569–39570, 39572, 39575 (in part), 39623, 39663, 39668–39671, 39673, 39675, 39685, 39752–39758, 39764, 39777, 39789 (in part), 39792–39794, 39796, 39798 (in part), 39799, 39801, 39803–39805, 39812, 39814–39815, 39819, 39821 (in part), 39822–39823, 39824 (in part), 39825, 39830, 39834, 39835 (in part), 39837–39838, 39840–39841, 39848, 39850, 39852, 39857, 39861 (in part), 39963–39967, 39978–39979, 39980 (in part), 39985, 45305, 45307, 45309–45311, 45313–45315, 45333–45335, 45341, 45344–45345, 45347–45348, 45350, 45353–45354, 45357, 45359–45361, 45363, 45366, 45373, 45375–45376, 45379, 45381–45382, 45383 (in part), 45384, 45388–45391, 45900, 45902–45905, ?45906, 45908, 45912, 45914–45915, 45918, 45920–45921, 45923–45925, 45929–45931, 45995 (in part), 45996 (in part), 45997 (in part), 46479, 46482–46483, 46486 (in part), 47008, 47010, 47012–47014, 47261, 47263–47265, 47269–47270, 49404, 49411, 49416, 49421–49422, 49425–49426, 49428, 49431, 49433, 49435–49437, 49439, 49478–49479, 49482–49483, 49486–49487, 49489–49490, 53797, 53803, 53805, 53807–53808, 53811, 53817, 53824, 53830, 53832, 53834, 54094, 54097, 54099, 54101–54102, 54105, 54116, 54119, 54122–54123, 54173, 54176–54178, 54184, 54189–54190, 54193, 54199, 60202. (San Jose Formation) CM 45974–45975, 45977–45978, 45979–45980, 45982, 45986, 45991–45992, 46808, 46817, 46830, 46841–46843, 46887, 46891–46893, 60568–60569, 60576, 60577–60582. ACM 11078. AMNH 4093, 4128, 16199, 86262, 86278,

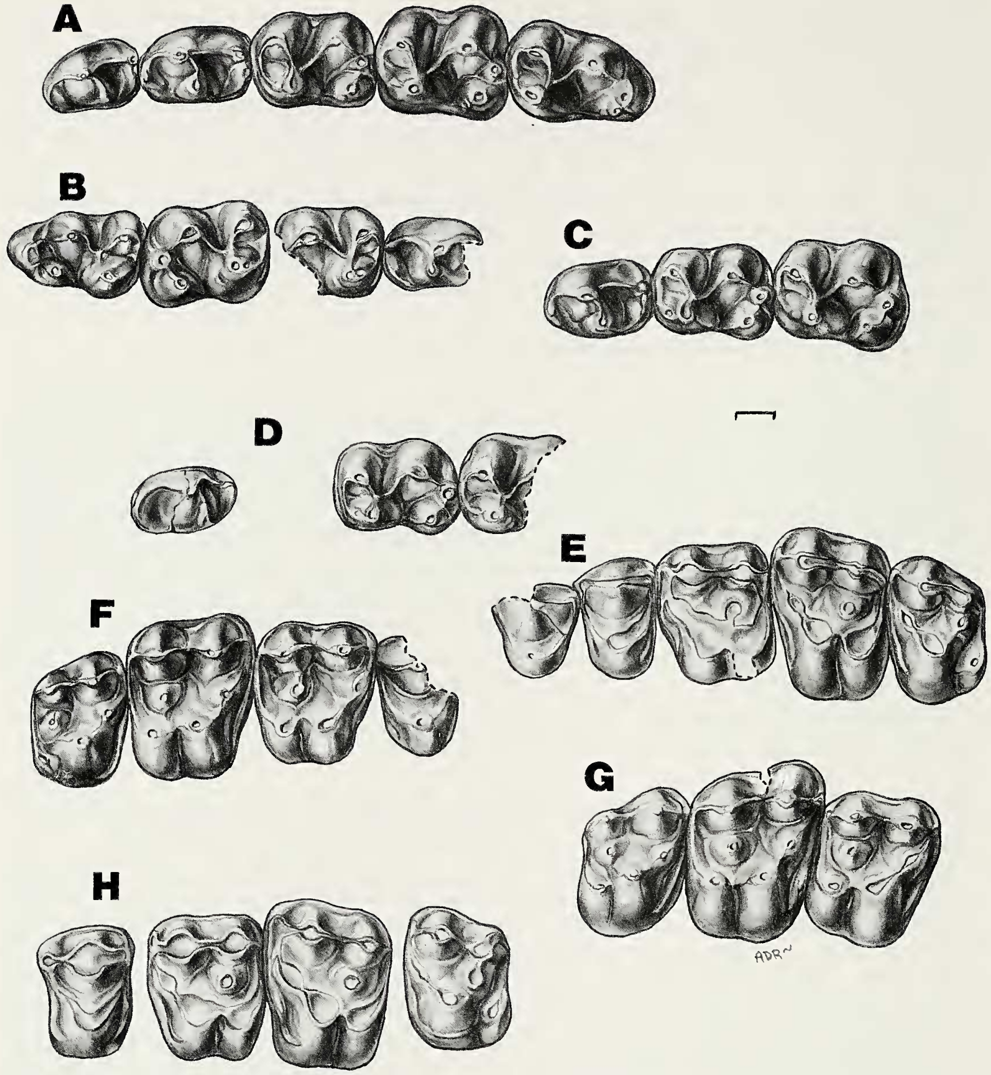

Fig. 9.—Specimens of *Hyopsodus paulus–lysitensis.* A, CM 22703 (lower); B, CM 28662; C, CM 54106; D, CM 19811; E, CM 21909; F, CM 22703 (upper); G, CM 39169; H, CM 39172. Scale equals 1 mm.

93330. (Bighorn Basin, Lysite) AMNH 15621. (Piceance Basin, tentatively referred) CM 4904–4905, 4910, 4916, 4939–4940, 34473.

Localities.—CM 111–112, 114, 118, 130, 793–794, 797, 800, 801–803, 805–807, 809–813, 877, 927–931, 941, 945, 964–966, 1007–1009, 1017–1019, 1021, 1025–1027, 1030–1031, 1033, 1064, 1091, 1903–1904, 1907, Scenery Gulch loc., Shooty Gulch loc. ACM Lysite localities. AMNH 15 Mile Creek loc., Bighorn Basin.

Known Distribution.—Lysitean of Wind River and Bighorn basins, Wyoming; late Graybullian through Lysitean of Piceance Basin, Colorado; ?late Graybullian/ ?early Lysitean of San Juan Basin, New Mexico.

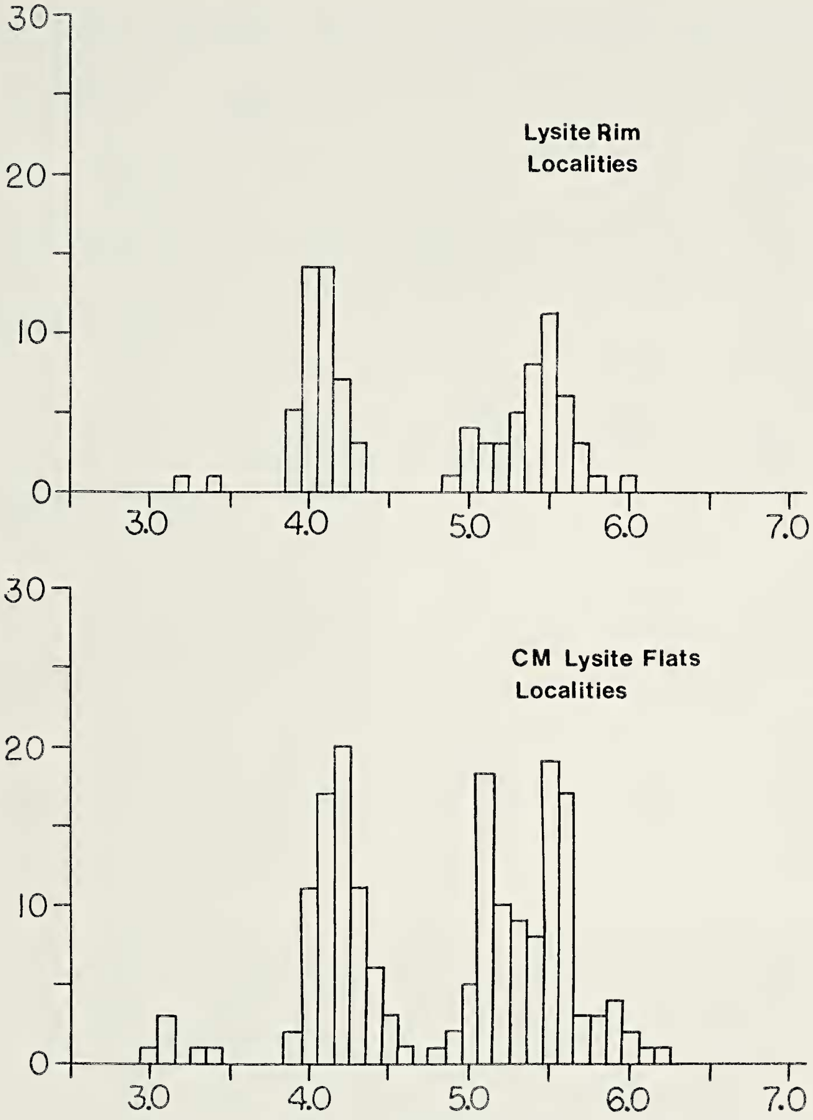

Fig. 10.—Frequency histograms for lower second molars of *Hyopsodus* from Wind River Formation Lysitean localities (second histogram combines all Lysite Flats localities). Vertical axis, number of individuals; horizontal axis, molar length in mm.

Discussion.—*Hyopsodus paulus–lysitensis* is intermediate between *H. paulus–simplex* and *H. paulus–wortmani* in the frequency and development of the following characters: more progressive than *H. paulus–simplex* in size of upper and lower third molars, distinctness of hypoconulid lobe and entoconid on M_3, lower molar paraconid less frequent in occurrence, upper molars somewhat less bunodont, hypocone more strongly expressed on M^3, hypocone more closely placed to protocone on M^{1-2} and better developed external cingula on molars and premolars. It differs from *H. paulus–wortmani* as outlined in the diagnosis above, but is very

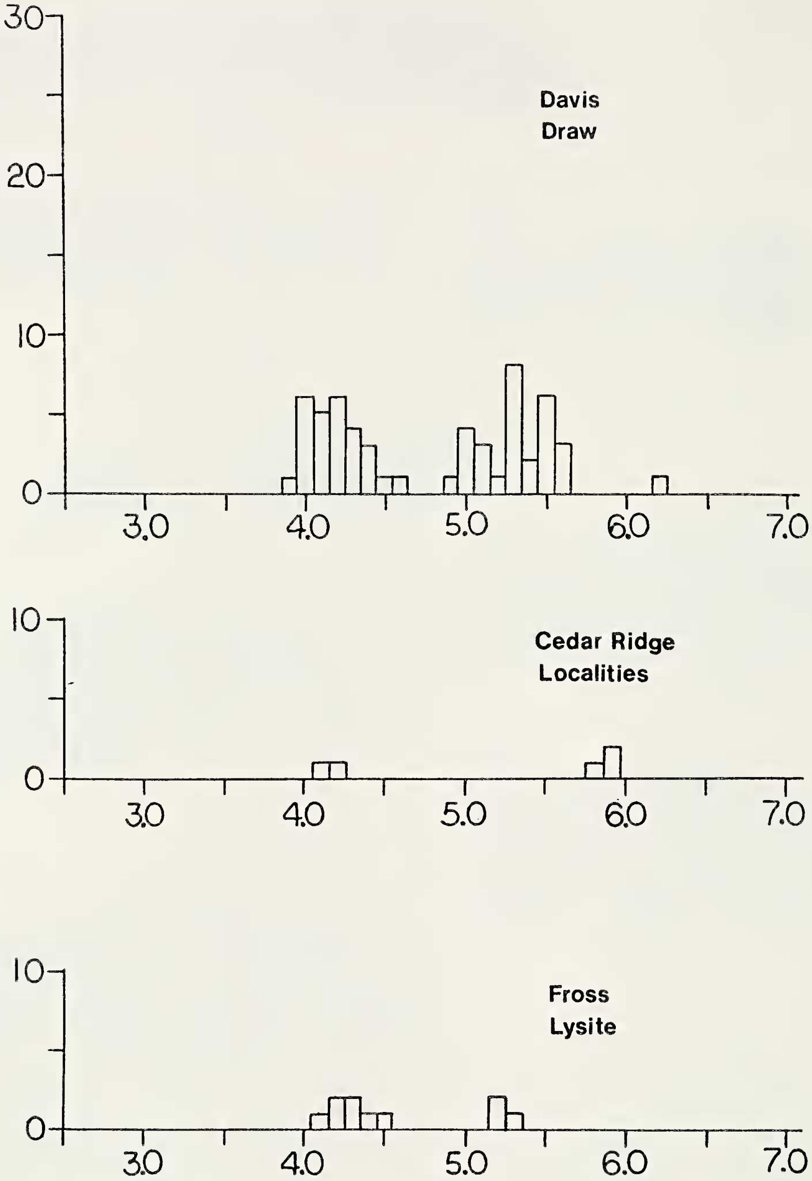

Fig. 11.—Frequency histograms for lower second molars of *Hyopsodus* from other Wind River Formation Lysitean localities. Vertical axis, number of individuals; horizontal axis, molar length in mm.

close to this segment in dental measurements (Tables 3, 4). Aside from relatively minor differences in the frequency of lower premolar morphology and the shorter relative length of M_3, these segments would be difficult to distinguish.

Guthrie (1967, 1971) referred Lostcabinian *H. paulus–wortmani* and Lysitean *H. paulus–lysitensis* material to the same species, *Hyopsodus miticulus.* The existence of an intermediate-sized lineage of *Hyopsodus* in the Lysite Member of the Wind River Formation has long been acknowledged. Kelley and Wood (1954)

Table 4.—Summary of statistics, upper dentitions of *Hyopsodus paulus* (lineage segments *H. paulus–paulus H. paulus–wortmani, H. paulus–lysitensis, H. paulus–simplex*). High, low, mean, SD in mm.

	P^3 (L, W)	P^4 (L, W)	M^1 (L, W)	M^2 (L, W)	M^3 (L, W)
H. paulus–paulus					
High	3.5, 3.6	3.3, 4.9	4.7, 5.5	5.1, 6.5	4.3, 5.5
Low	3.1, 3.2	2.9, 4.0	3.7, 4.6	4.1, 5.5	3.6, 4.3
n	4	13	23	37	27
Mean	3.3, 3.4	3.2, 4.4	4.2, 5.0	4.5, 5.9	3.9, 5.0
SD	0.15, 0.14	0.12, 0.23	0.22, 0.26	0.22, 0.26	0.19, 0.29
CV	4.5, 4.1	3.8, 5.2	5.2, 5.2	4.9, 4.4	4.9, 5.8
H. paulus–wortmani					
High	3.4, 3.4	3.1, 4.4	4.4, 5.1	4.8, 6.1	3.6, 4.9
Low	3.0, 3.1	2.7, 3.7	3.5, 4.1	3.6, 4.9	3.0, 4.1
n	5	10	16	21	10
Mean	3.1, 3.2	2.9, 4.1	3.8, 4.6	4.1, 5.5	3.4, 4.6
SD	0.17, 0.10	0.11, 0.20	0.27, 0.31	0.29, 0.35	0.19, 0.21
CV	5.5, 3.1	3.8, 4.9	7.1, 6.7	7.1, 6.4	5.6, 4.6
H. paulus–lysitensis					
High	3.5, 3.6	3.5, 4.6	4.6, 5.6	4.7, 6.1	4.1, 5.6
Low	2.5, 3.1	2.9, 3.9	3.5, 4.3	3.6, 4.9	3.1, 4.2
n	6	19	22	36	25
Mean	3.2, 3.3	3.2, 4.2	3.9, 4.8	4.1, 5.5	3.4, 4.6
SD	0.34, 0.16	0.17, 0.20	0.29, 0.32	0.27, 0.32	0.22, 0.32
CV	10.6, 4.8	5.3, 4.8	7.4, 6.7	6.6, 5.8	6.5, 7.0
H. paulus–simplex					
High	3.1, 3.1	3.3, 4.5	3.9, 5.1	4.3, 5.9	3.5, 4.5
Low	— —	2.9, 4.0	3.4, 4.3	3.6, 5.0	2.6, 3.8
n	1	12	14	22	20
Mean	— —	3.0, 4.2	3.6, 4.6	3.9, 5.5	2.9, 4.1
SD	— —	0.12, 0.19	0.13, 0.19	0.17, 0.21	0.21, 0.22
CV	— —	4.0, 4.5	3.6, 4.1	4.4, 3.8	7.2, 5.4

assigned specimens of this lineage to *H. mentalis,* while Guthrie (1967) believed that the size of Lysite Member specimens agrees better with *H. miticulus.* Analysis of CM and AMNH New Mexican material suggests that Almagre and Largo "*Hyopsodus miticulus*" and some specimens of "*H. mentalis*" are similar to Wind River Lysite material, but show a slightly different distribution of character states and size distribution. Since the holotypes of both these species are lost, these names are probably best not applied to Lysite Member material. The subspecies *H. mentalis lysitensis* (type, AMNH 15621) from Lysite beds of the Bighorn Basin was designated as a Lysite form of intermediate-sized *Hyopsodus* by Matthew (1915*b*). The lineage-segment etymology chosen here reflects his observations. The morphology of the holotype is that most typical of Lysitean *H. paulus.*

In the Lysitean of the Wind River (refer to histograms in Fig. 10, 11) and Bighorn basins, *Hyopsodus paulus–lysitensis* coexists in lithosympatry with both the smaller *Hyopsodus minor* and the significantly larger *Hyopsodus powellianus–powellianus.* In the Piceance and San Juan basins (Fig. 21), it again is found in association with *H. minor* and a form generally larger than *H. paulus–lysitensis,* but smaller than *H. powellianus–powellianus. Hyopsodus paulus–lysitensis* from these more southern basins is referred to *H. paulus–lysitensis* separately above, by geographic area. This was done because of their slightly more bunodont, inflated molar cusps and somewhat less open molar talonids (much closer to *H. paulus–lysitensis* than to *H. paulus–simplex*) in the majority of specimens. In the San Juan Basin, lower dentitions from the Almagre level are distinct from Largo specimens in the primitively shorter length of M_3. Some of these differences may be attributable to anagenesis or possibly regional variation.

Variation within *H. paulus–lysitensis* from the Lysite Member of the Wind River Formation includes some individuals that partially overlap both immediately older and younger lineage segments of *H. paulus*. For example, CM 54106 primitively features a well-developed paraconid on M_1 and a shorter, more rounded P_4 with less well-developed hypocrista and hypoconid. On the other hand, CM 22703 and CM 39472 are more gracile, have a longer M_3 and more open, notched talonids on M_{1-3}. Similar variation was noticed in Lysite *Hyopsodus* from the Amherst collections by Kelley and Wood (1954).

Hyopsodus paulus–lysitensis shares with penecontemporaneous *H. powellianus–powellianus* a well-basined, very rarely notched P_4 with frequently strong posthypocristid, larger third molars, variably distinct P_4 metaconid, and strong upper molar protoloph. It differs in the more frequent occurrence of molar metastylids, less anteriorly placed molar protoconid, more commonly distinct premolar paraconid, less expanded anterior cingula on M^{1-3}, M^3 hypocone and hypocrista structure, and significantly smaller size. *Hyopsodus minor* is considerably smaller than *Hyopsodus paulus–lysitensis* and has more poorly differentiated, conical cusps and less molariform premolars. In the San Juan and Piceance basins, referred specimens of *H. paulus–lysitensis* differ from *H.* sp., cf. *H. mentalis* primarily in their smaller size and in lacking wide P_4 talonids and frequently large entoconids.

Lineage Segment *Hyopsodus paulus–simplex*
(Fig. 12, 13; Tables 3, 4)

Diagnosis.—Most bunodont lineage segment of *Hyopsodus paulus*. Slightly smaller in average length of M_2 than *H. paulus–lysitensis*. Compared to all other North American *Hyopsodus* except *H. loomisi*, lower molar trigonid and talonid cusps blunt and unelevated; talonids poorly formed and unnotched. M_3 smaller than in later lineage segments of *H. paulus*. Premolars somewhat longer but less basined than in *H. paulus–lysitensis*. Compared to later *H. paulus*: P_{3-4} hypocristid and hypoconid poorly developed, paraconid more frequently present on M_1 and often on M_2, metastylid and entostylid more common. M^3 metacone, metaconule, and hypocrista stronger and more distinct than in penecontemporaneous *Hyopsodus loomisi*. Labial and anterior cingula and external ribs of M^{1-3} less developed than in *H. paulus–lysitensis*. In contrast to *H. loomisi*, molar paraconule and protocone elevated above the level of the low anterior cingula. Molar hypocone smaller and more distolabially situated than in *H. paulus–lysitensis*; more robust than in *Hyopsodus loomisi*.

Diagnostic Series.—ACM 2290 (type, *Hyopsodus simplex*), 10108. CM 11478, 12120, 12379, 12404, 28998, 36728, 39427, 57991, 58082, 58093.

Referred Specimens. CM 11464, 11467–11468, 11470, 11478, 12115–12116, 12119–12120, 12185, 12198, 12208, 12224, 12226, 12270, 12273, 12275, 12305, 12344, 12355–12356, 12359, ?12362, 12376–12379, 12382, 12384, 12386, 12404, 12413–12414, 12418, 17466, 34315 (in part), 34373, 34380, 34383, 34391, ?34404, 34415, 34419, 34426, 36118–36119, 36127, ?36131, 36133, 36227, ?36230, 36233, 36235, ?36236, 36237, 36239, 36243, 36246, 36248–36250, 36252, 36548, 36551, 36615, 36617–36620, 36622, ?36623, 36624, 36706–36707, 36710–36711, 36713–36714, 36717–

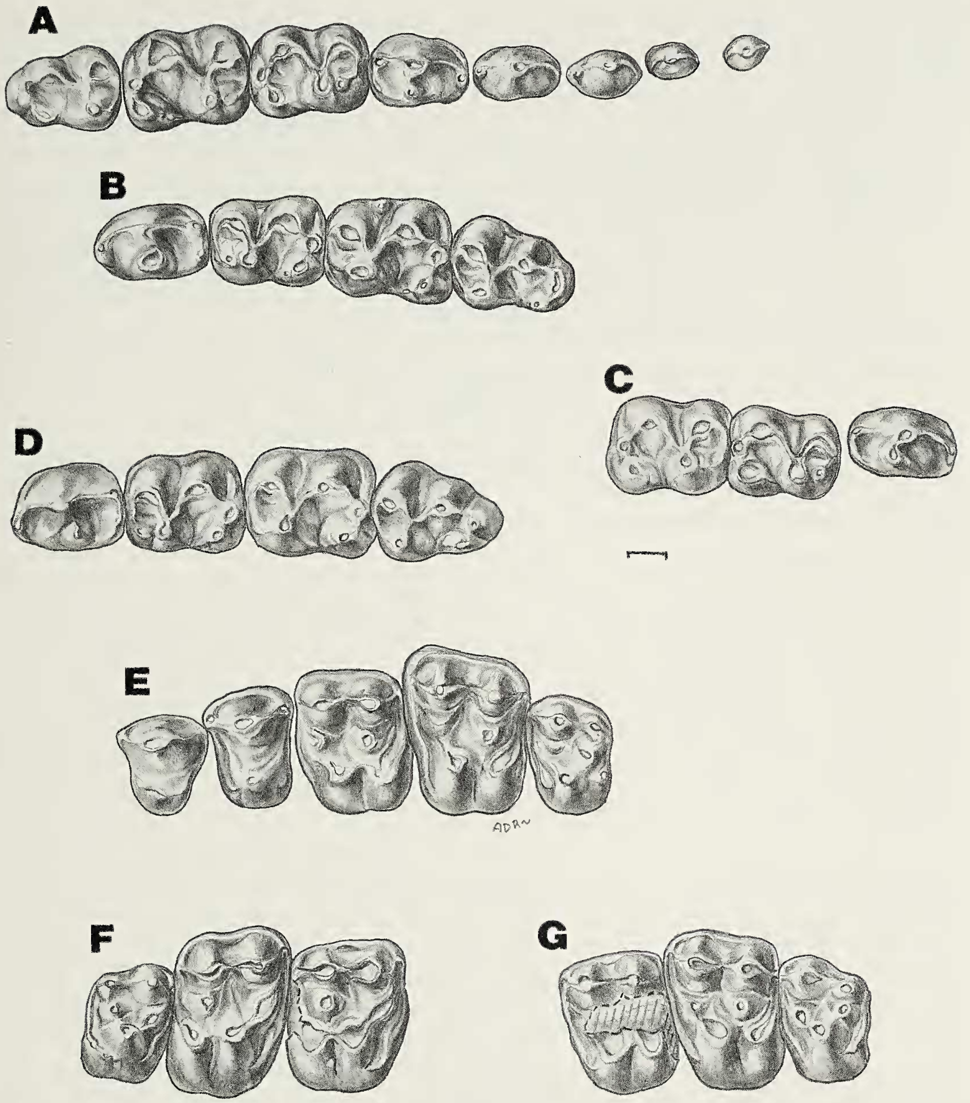

Fig. 12.—Specimens of *Hyopsodus paulus–simplex.* A, CM 12404 (lower); B, CM 58093; C, CM 12376; D, CM 57991; E, CM 12404; F, CM 11478; G, CM 58082. Scale equals 1 mm.

36718, 36720, 36723, 36728–36731, 36733, ?36735, 36742–36746, 36749, 36751–36752, 36756, 39418 (in part), 39420 (in part), 39421 (in part), 39422, 39423 (in part), 39427, 39428 (in part), 39429 (in part), 39430 (in part), 39431, 39432 (in part), 39433 (in part), 39434, 39442 (in part), 39443 (in part), 39444 (in part), 39445 (in part), 39446 (in part), 39447 (in part), 39448 (in part), 39449 (in part), 39450 (in part), 39451 (in part), 39453, 39455, 39456 (in part), 39457–39459, 39460 (in part), 39462 (in part), 39463 (in part), 46646, 51985, ?51987, 51988–51989, 51992, 51994–51998, 53708, 53710, 53713, 53737, 53869, 53913, ?53926, 57955–57956, 57958, 57963, 57991, 58082, ?58083, 58084, 58086, 58088, 58090–58098, 58101, 58107, 58109–58111, 58207–58210, 58213–58214, ?58217, 58220–58221. ACM 2290 (type, *H. simplex*), 6025, 10108, 10294.

Localities.—CM 140–157, 873, 953, Dorsey Creek loc. ACM Tatman Mountain, Clark's Fork Basin Graybull beds.

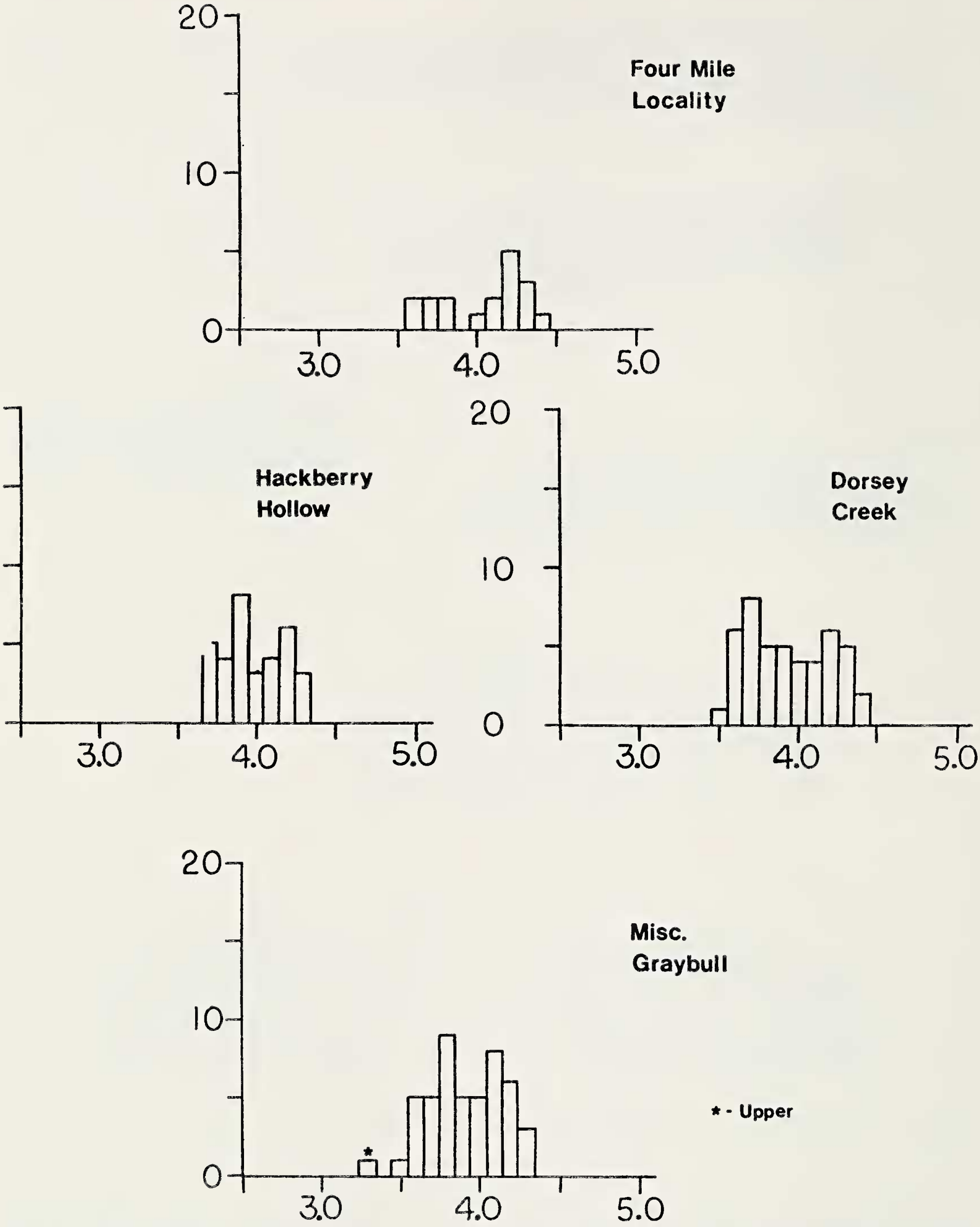

Fig. 13.—Frequency histograms for lower second molars of early Eocene *Hyopsodus*. Four Mile locality is considered earliest Eocene (Sandcouleean), others Graybullian. Vertical axis, number of individuals; horizontal axis, molar length in mm.

Known Distribution.—Sandcouleean through Graybullian of Bighorn Basin and Clark's Fork Basin, Wyoming; earliest Eocene beds of Wasatch Formation, Washakie Basin, northwestern Colorado.

Discussion.—The taxonomic status of this lineage segment is based on the holotype of *H. simplex* (ACM 2290) only; although its specific locality is unknown, it well represents the average morphology of *H. paulus* from the Graybullian Land Mammal Subage. As outlined by McKenna (1960), specimens from the Sand Coulee area referred to *Hyopsodus simplex* by Matthew (1915*b*) belong to a distinct taxon, *Hyopsodus loomisi.* AMNH 16842, illustrated as *H. simplex* by Matthew, also appears to be a specimen of *Hyopsodus loomisi.* Although confusing, "simplex" is chosen as a segment name here because no other names with formal priority are available; *H. miticulus* is likely to be a more anagenetically progressive form from a distant basin whose type is lost.

Early to middle Graybullian specimens agree in morphology with the type of *H. simplex* and are not as similar to any CM or AMNH dentitions examined from the Almagre and Largo localities of the San Juan Basin (refer to discussion of the concept of species *Hyopsodus paulus*).

Gingerich (1974*a*) suggested the presence of three lineages of *Hyopsodus* gradually diverging in size in the Graybullian of the Willwood Formation. Data presented here indicates that the two smaller lineages may be delineated based on morphology (compare diagnoses of *H. paulus–simplex* with *H. loomisi*). The size divergence of two small to medium-sized taxa noted by Gingerich is possibly confirmed by the much closer clustering of M_2 length between *H. paulus* and *H. loomisi* (the larger representing *H. paulus–simplex*) at the comparatively earlier Graybullian CM loc. 873 versus the somewhat later CM Dorsey Creek localities (see Fig. 13). Character overlap is also greater at CM loc. 873; CM 57991 is similar to *H. loomisi* in its poorly differentiated entoconid on M_2, but otherwise is much closer to the diagnosis of *H. paulus–simplex.* Contrary to Gingerich (1989), a slight groove separating the molar protoconid from the metaconid does not distinguish *Hyopsodus loomisi*; it is shared by *H. paulus–simplex* and *H. loomisi* and is a function of the larger lingual trigonid area common to all Graybullian and earlier *Hyopsodus.*

Hyopsodus paulus–simplex is the most commonly occurring lineage of *Hyopsodus* at most Graybullian localities, but is closely approached in abundance by *Hyopsodus loomisi* at Dorsey Creek and CM loc. 873. Although there is some overlap, *H. paulus–simplex* can be recognized by larger average size, a larger, more lingually protruding entoconid on the lower molars, transversely shorter P^{3-4}, and better developed upper molar hypocones and M^3 labial cusps, and labial and anterior cingula. Although its size may be very similar to *H. loomisi,* these characters delineate the segment as early as the Sandcouleean. Primitive characters shared in common with *H. loomisi* include low-crowned cusps on dentitions, poorly developed lophs, cristid obliqua on M_{1-3} meets trigonid more labially, lack of distinct lower premolar anterior and lingual cusp, weak to no basining of P_{3-4} talonid, and small third molars. The high frequency of presence of the lower molar paraconid, sometimes with a distinct base, is also common to Graybullian *Hyopsodus* in general.

One highly variable feature is the shape of the hypoconulid/entoconid on M_3, which may appear as an arcuate lobe, as two cusps or multiple cusps (as in ACM 16842). In general, the posterior M_3 cusps of *Hyopsodus* specimens are rarely consistent in these types of morphologic detail; "accessory cusps" are common and more probably indicate ontogenetic disturbance (Redline, 1990*b*). *Diacodexis* shows similar variation (Krishtalka and Stucky, 1985:426). Usually, the length of the tooth and degree of development of the primary cusps are most diagnostically useful. In *Hyopsodus paulus–simplex,* M_3 is universally short and low crowned, like the type of *Hyopsodus simplex.*

Hyopsodus paulus–simplex is the most primitive known lineage segment of *Hyopsodus paulus,* but appears derived or, alternatively, anagenetically advanced with respect to *Hyopsodus loomisi.* At its first occurrence, it already possesses the larger lower premolars, robust molar entoconids, and more distinct upper molar hypocones and cingula typical of pre-Bridgerian *Hyopsodus.* Were it not for the co-occurrence of both *H. paulus–simplex* and *H. loomisi* in the Sandcouleean and throughout the early to middle Graybullian and upper P^4 differences, *H. loomisi* might simply be considered a most primitive form of *H. paulus.*

Hyopsodus minusculus Leidy, 1873
(Fig. 5, 14; Table 5)

Holotype.—ANSP 10259. Partial LP^4, LM^{1-3}. Collected from Dry Creek, Bridger Formation, Bridger Basin, Wyoming.

Diagnosis.—Very small size compared to other *Hyopsodus*; mean length of M_2 in the Wind River Basin, 3.5 mm. Compared to *H. paulus–paulus,* M^{1-2} more nearly square; (length/width ratio closer to one); M^1 closer in occlusal area to M^2; M^{1-2} paraconule smaller, base not distinct, more confluent with protoloph. Compared to all *H. paulus,* distinctly more ridge-like hypocrista with very small or absent hypocone on M^3; hypocrista wraps more anterolingually around protocone base, often approaching or joining the anterior cingulum. External cingula more frequently well expressed on upper premolars and molars; in contrast to *H. paulus–paulus,* often completely wraps around labial margin of teeth. Compared to other Wasatchian or early Bridgerian *Hyopsodus,* P_{3-4} shorter, protocone and hypocristid much higher than lingual margin of teeth. Compared to *H. paulus, H. minor,* and *H. powellianus,* P_4 talonid more weakly basined, notched, with no trace of entoconid; paraconid weaker, with preparacristid anteriorly shifted close to protoconid and metaconid somewhat posteriorly placed. Lower molars appear more elongate than in *H. paulus*; M_{1-2} hypoconulid smaller and posteriorly shifted; base of entoconid more closely appressed to hypoconulid. M_{1-3} metastylid and entostylid more rare than in *H. paulus–paulus.* Molar cristid obliqua joins trigonid more labially than in *H. paulus–paulus.*

Diagnostic Series.—ANSP 10259 (type, *Hyopsodus minusculus*). AMNH 12496, 14623. CM 21050, 22339, 27442, 29124, 29128, 30928, 40618, 44916.

Referred Specimens.—CM ?4950, 4951–4952, 21012, 21044 (in part), 21045, 21047, 21050, 21053, 21055, 21061, 21064, 21071–21072, 21077, 21079–21080, 21086–21087, 21090, 21093–21094, 21099–21100, 21102, 21106, 21923, 21926, 22319, 22339–22341, 22343, 22530, 22531 (in part), 27438, 27440–27446, 29123–29124, 29127–29129, 29131, 29135 (in part), 30892, 30894, 30896–30897, 30901–30902, 30905, 30907–30908, 30910–30915, 30918, 30922–30924, 30928–30929, 30934, 31003, 31005–31006, 31009, 31011–31012, 31329, ?35742, 35758–35759, 35761–35770, ?36447, 36448, 36943–36944, 37331 (in part), 37332 (in part), 40080, 40084, 40089–40091, 40093, 40095–40097, 40616, 40626–40628, 40631–40632, 40634–40635, 40637–40639, 40641–40644, 40646, 40648–40649, 40651–40652, 40654, 40656, 40658, 40660, 40663–40664, 40676, 41618, 44916, 44919–44922, 44923 (in part), 44924–44929, 44938, 44941–44943, 44945, 44947–44954, 44956 (in part), 44959, 44961–44962, 44971, 44974 (in part), 44976–44977, 44983 (in part), 44991–44992, 44997, 45166, 45190, 45322–45324, 45958, 45960, 45962, 45965, ?45967, 45971, 46658, 47117–47119, 47223, 47239, 55035, 55039, 55048, 55050, 55052, 55055–55056, 55058, 55061–55062, 55065–55066, 55071, 55073, 55075, 55078, 55080–55081, 55084–55085, 55219–55220, 55223–55224, 55226, 55230, ?55231, ?55232, 55235–55237, 55239, 55242–55245, 55247, 55253–55254, 55257, 55261–55265, 55273, 55275, 55280–55282, 55286–55288, 55290–55291, 55294, 55298, 55302–55303, 55305–55306, 55312–55313, 55315, 55318, 55320–55321, 55323, 55325,

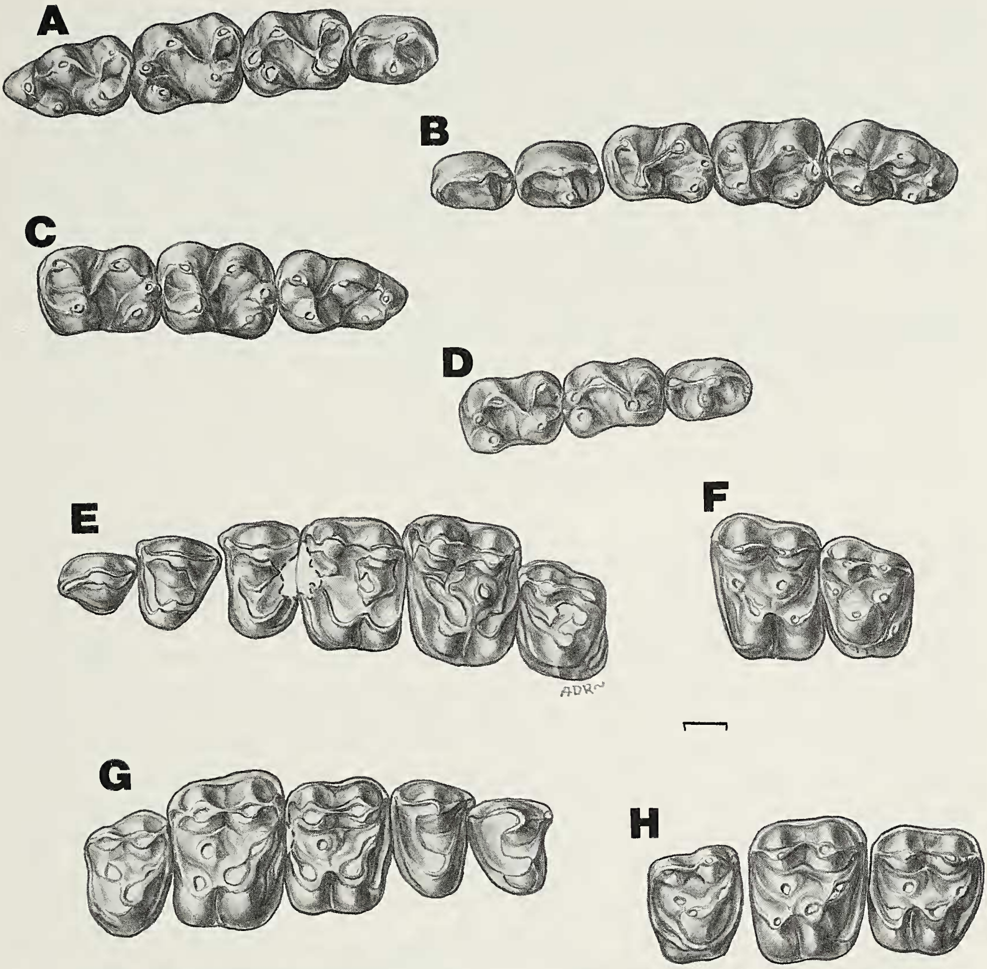

Fig. 14.—Specimens of *Hyopsodus minusculus.* A, CM 21050; B, CM 40080; C, CM 21061; D, CM 36447; E, CM 56236; F, CM 44945; G, CM 22339; H, CM 22339 (separate specimen). Scale equals 1 mm.

55327–55328. UCM 42820, ?42840, ?42868, 42871, 45364, 45537, 45552, 46590. UW 23534, 23536. AMNH 12496, 14612–14613, 14623–14624. ANSP 10259 (type, *H. minusculus*).

Localities.—CM 34, 1036, 1038, 1543, 1545, 1548. UCM 80064, 80065, 81026. UW V89041. AMNH "Lost Cabin Beds"; 4 mi S of Granger, Wyoming, loc. (Blacksforkian). ANSP loc. Dry Creek, Wyoming (Blacksforkian).

Known Distribution.—Earliest Bridgerian (Gardnerbuttean) of Wind River Basin, Wyoming; Huerfano Basin, Colorado; Blacksforkian of western North America.

Discussion.—This marks the first time small-sized *Hyopsodus* from the Wind River Basin (as well as the Gardnerbuttean of the Huerfano) have been referred to *Hyopsodus minusculus.* As in *H. paulus, H. minusculus* from the Gardnerbuttean of the Lost Cabin Member is morphologically close to the types and referred specimens from the younger Blacksforkian localities. CM 55236 possesses a P^2

Table 5.—Summary of statstistics, lower and upper dentitions of *Hyopsodus minusculus*. High, low, mean, SD in mm.

	P_3 (L, W)	P_4 (L, W)	M_1 (L, W)	M_2 (L, W)	M_3 (L, W0
High	2.7, 2.0	3.2, 2.6	3.5, 3.0	3.9, 3.3	4.1, 3.1
Low	2.3, 1.6	2.6, 2.0	3.1, 2.3	3.1, 2.5	3.4, 2.2
n	11	43	70	112	72
Mean	2.5, 1.8	2.8, 2.2	3.3, 2.6	3.5, 3.0	3.9, 2.6
SD	0.11, 0.12	0.17, 0.15	0.11, 0.16	0.11, 0.19	0.16, 0.17
CV	4.4, 6.7	6.1, 6.8	3.3, 6.2	3.1, 6.3	4.1, 6.5
	P^3 (L, W)	P^4 (L, W)	M^1 (L, W)	M^2 (L, W)	M^3 (L, W)
High	3.0, 3.0	2.8, 3.9	3.8, 4.3	4.0, 5.1	3.2, 4.1
Low	2.2, 2.5	2.3, 3.0	3.1, 3.4	3.1, 4.1	2.5, 3.2
n	6	11	21	29	25
Mean	2.5, 2.6	2.6, 3.4	3.4, 3.9	3.5, 4.5	2.8, 3.7
SD	0.25, 0.35	0.14, 0.24	0.17, 0.21	0.20, 0.23	0.19, 0.26
CV	10.0, 13.5	5.4, 7.1	5.0, 5.4	5.7, 5.1	6.8, 7.0

with a lingually expanded inner surface, somewhat more typical of later *Hyopsodus* (see Gazin, 1968:45) than of Wasatchian lineages. Similar-sized CM 40660 does not feature the lingual expansion, varying toward the primitive condition.

An insufficient number of Blacksforkian specimens were examined to allow division of *Hyopsodus minusculus* into successive lineage segments. Specimens from the uppermost Wind River Formation referred to *H. minusculus* share with later Bridgerian material the derived characters listed in the diagnosis. West (1979*a*) concluded that *H. minusculus* did not survive beyond the time of Bridger B deposition, but noted regional variation in the relative abundance of small specimens from various Blacksforkian localities. In earliest Bridgerian sediments of the Wind River Basin, *H. minusculus* is extremely common, identifiable dentitions being as numerous as the intermediate-sized *Hyopsodus paulus.* As will be discussed later, this pattern supports the conclusion that different-sized lineages of *Hyopsodus* were environmentally specific.

Recently, specimens of *H. minusculus* have also been recovered from the southern Wind River Basin in the vicinity of Oil Mountain, Fremont County (UW loc. V89041). Along with associated *H. paulus,* this record supports preliminary observations that the locality is earliest Bridgerian in age (J. Amos, University of Wyoming, personal communication). It also confirms that the occurrence of non-overlapping populations of *H. paulus* and *H. minusculus* marks the onset of the earliest Bridgerian.

Like *H. paulus–paulus, Hyopsodus minusculus* appears to be less variable in character expression than comparable Wasatchian species or lineage segments. There is virtually no size (Fig. 6) or morphologic overlap with the Gardnerbuttean or Blacksforkian *H. paulus* lineage segment. Overlap, however, does occur with a number of Lostcabinian specimens of *H. paulus–wortmani* (see discussion of lineage segment *H. paulus–wortmani*). For instance, CM 30928 has a well-developed M^3 hypocone, more typical of *H. paulus–wortmani,* but one that is part of a strongly developed, anteriorly tracing hypocrista, as in *H. minusculus.* Again, *H. paulus–paulus* shows similar overlap with *H. paulus–wortmani,* suggesting a common origin for both *H. minusculus* and *H. paulus–paulus.*

Hyopsodus minusculus is similar in size to the late Graybullian through Lysitean species *Hyopsodus minor,* but no derived characters (other than overall size) suggest a relationship between these two small-sized lineages. *Hyopsodus minusculus* shares lophodont molars, shortened premolars, and transversely compressed premolar paracones, among other characters, with lineage segment *H. paulus–wortmani,* while being derived in lower premolar talonid structure and molar shape and structure as detailed in the diagnosis. *Hyopsodus minor* shares primitive features with *Hyopsodus loomisi,* and to a degree with *H. paulus–simplex,* and is distinct in morphology from *H. minusculus.* Additionally, *Hyopsodus minor,* or a suitable intermediate between *H. minor* and *H. minusculus,* is not known from the Lostcabinian of the Wind River Basin, nor apparently from the Willwood Formation Lostcabinian (size data of Gingerich, 1974*a*).

The pattern of *Hyopsodus* phylogeny suggests that two small *Hyopsodus* lineages, *H. minor* and *H. minusculus,* iteratively diverged in the early Eocene. The first evolved in the early Wasatchian (discussed below) and the second at the close of the Wasatchian.

Hyopsodus minor Loomis, 1905
(Fig. 10, 11, 15; Table 6)

Hyopsodus wortmani minor Matthew, 1915*b*.

Holotype.—ACM 3492. RM_{1-3}. Collected from Lysite Beds, Wind River Formation, Wind River Basin, Wyoming.

Diagnosis.—Very small size compared to other *Hyopsodus,* smallest species of *Hyopsodus.* Molar conules smaller than in *H. minusculus.* M^{1-2} hypocone small with base restricted in size and more separated from protocone than in other *Hyopsodus.* M^3 relatively more square than in *H. minusculus*; hypocrista wide and more posteriorly situated. M^3 protocone and axis of trigon centrally located; crown is most anteroposteriorly symmetrical of *Hyopsodus* species. Labial ribs and ectocingula (particularly immediately labial to molar metacone) less distinct than in penecontemporaneous *H. paulus–lysitensis,* better developed than in *H. loomisi* and *H. paulus–simplex.* Differs from *H. minusculus* in having talonids somewhat basined with entoconid on P_4; and with lower premolar metaconids more anteriorly placed. M_{1-3} paraconid variably present, less common than in other Lysitean *Hyopsodus.* In contrast to other *Hyopsodus* except *H. loomisi,* entoconid and hypoconulid on M_{1-2} are restricted, with merged bases, and rarely extend more lingually than trigonid. Anterior cingulids of lower molars weaker than in other *Hyopsodus.*

Diagnostic Series.—ACM 3492 (type, *Hyopsodus minor*). CM 9966, 12151, 22699, 39865, 49400, 49415, 49432.

Referred Specimens.—CM 4904, 9779, 9966, 10471–10473, 12151, 12242, 19819, 20941, 22693 (in part), 22699, ?39175, 39185, 39196, 39289, ?39486, 39526, 39529, 39800, ?39820, 39861 (in part), 40692–40693, 45332, 45351, 45370–45371, 45934, 45955, 45976, 45992, 45995 (in part), 45997 (in part), 46815–46816, 46850, 49400, 49408, 49415, 49427, 49430, 49432, 49434, 60567, 60584–60586, ?60587. ACM 2308, 3492 (type, *H. minor*).

Localities.—CM 112, 118, 130, 142, 793, 797, 800, 802, 806, 811, 813, 928, 931, ?936, 1007, 1021, 1025, 1064, 1091, 1903, DeBeque Fm., nonspecific horizon. ACM Lysite Beds (Loomis collection).

Known Distribution.—Late Graybullian through Lysitean of Bighorn Basin, Wyoming; ?late Graybullian/?early Lysitean of Piceance Basin, Colorado, and San Juan Basin, New Mexico; ?early Lysitean through Lysitean of Wind River Basin, Wyoming. ?Late Lysitean/?early Lostcabinian of Wind River Basin, Wyoming.

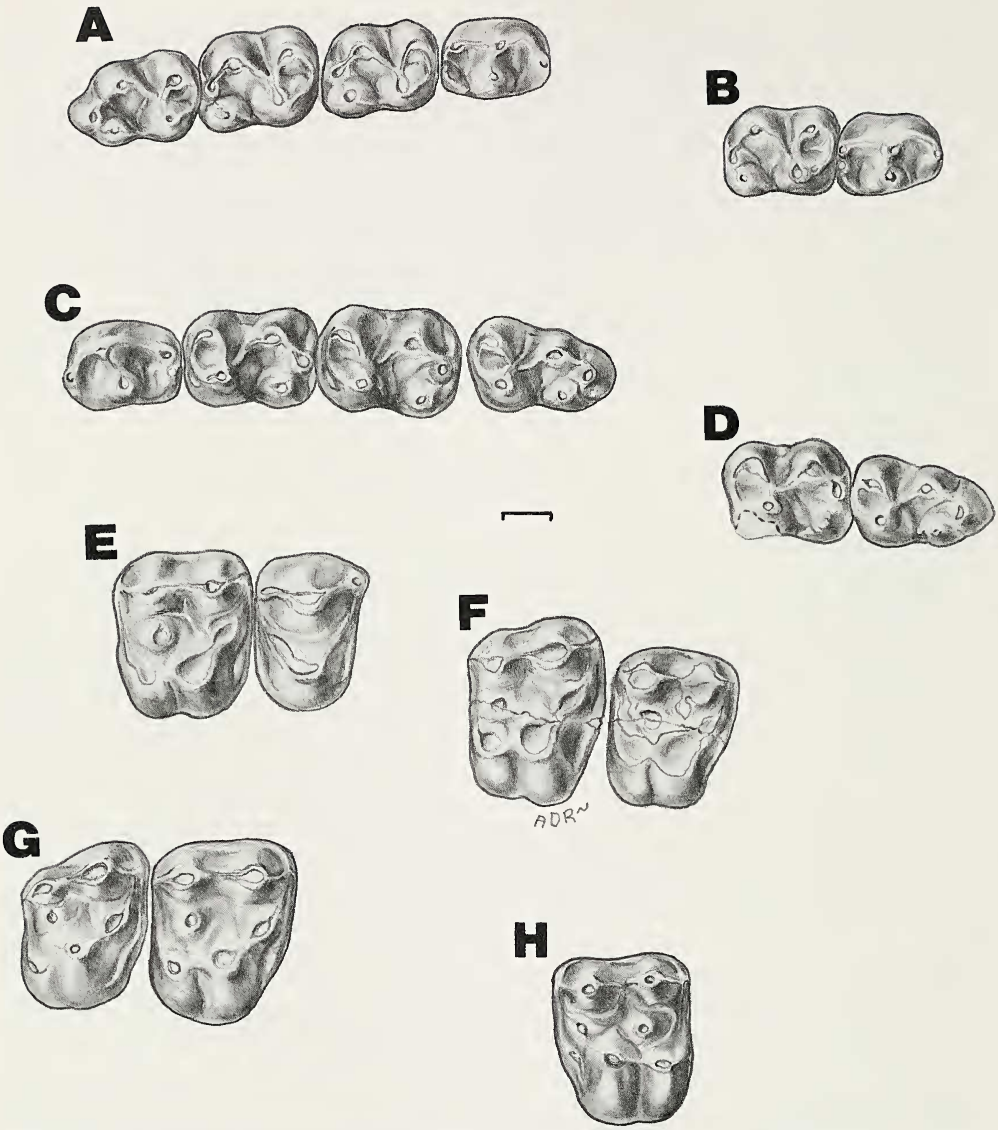

Fig. 15.—Specimens of *Hyopsodus minor*. A, CM 49400; B, CM 22699; C, CM 19819; D, CM 45371; E, CM 22694; F, CM 20941; G, CM 28752; H, CM 28668. Scale equals 1 mm.

Discussion.—Hyopsodus minor is a relatively rare constituent of the Lysite fauna of the Wind River Basin but is far more plentiful in the Lysitean of the Bighorn Basin (*H. wortmani* of Gazin, 1968). At the time of Kelley and Wood's (1954) revision, the holotype was the only known specimen. Matthew (1915*b*) referred other material from the AMNH collections to *H. wortmani ?minor* but suggested these dentitions showed elongate, high-cusped molars. No specimens with this morphology are present in the very large CM and ACM Lysite Member collections examined for this study. More recent collecting in the Lysite Member has produced new material of *Hyopsodus minor,* enabling a more complete di-

Table 6.—Summary of statistics, lower and upper dentitions of *Hyopsodus minor*. High, low, mean, SD in mm.

	P_3 (L, W)	P_4 (L, W)	M_1 (L, W)	M_2 (L, W)	M_3 (L, W)
High	2.7, 2.1	3.2, 2.4	3.3, 2.7	3.4, 3.1	3.7, 2.8
Low	2.4, 1.9	2.6, 1.8	2.9, 2.3	3.0, 2.4	3.4, 2.2
n	3	10	15	16	12
Mean	2.5, 2.0	2.8, 2.1	3.0, 2.5	3.2, 2.7	3.5, 2.4
SD	0.12, 0.09	0.20, 0.16	0.11, 0.11	0.13, 0.17	0.08, 0.16
CV	4.8, 4.5	7.1, 7.6	3.7, 4.4	4.1, 6.3	2.3, 6.7
	P^3 (L, W)	P^4 (L, W)	m^1(L, W)	m^2(L, W)	m^3(L, W)
High	— —	3.0, 4.0	3.5, 4.4	3.8, 4.8	3.4, 4.3
Low	— —	— —	3.0, 3.7	2.9, 3.5	2.2, 3.4
n	—	1	6	6	3
Mean	— —	— —	3.3, 4.2	3.4, 4.4	2.9, 3.9
SD	— —	— —	0.17, 0.26	0.32, 0.46	0.54, 0.40
CV	— —	— —	5.2, 6.2	9.4, 10.3	18.6, 10.3

agnosis. The upper dentition is still too incompletely known for confident identification; in fact, the high coefficient of variation for upper teeth of *Hyopsodus minor* (Table 6) indicates that some specimens referred here to *H. minor* might be *H. paulus.* In contrast to the upper dentition, there is less variability in the morphology of lower dentitions of *Hyopsodus minor.* This low level of variation may be attributable in part to the limited number of specimens (a larger number might suggest variation in teeth not well represented by the CM sample) or their restricted geographic provenance. A similar phenomenon is also apparent in the relatively rare *Hyopsodus powellianus–walcottianus* lineage segment discussed later.

Differing from the Lysite Member of the Wind River Basin, *Hyopsodus minor* (Fig. 23) is more common in the San Juan and Piceance basins. In the Bighorn Basin, two specimens (CM 12151 and 12262) from the Willwood Formation bearing labels marked "upper Graybull" closely meet the diagnosis of *Hyopsodus minor,* except for a proportionately smaller M^3 in CM 12151. The new species, *Hyopsodus pauxillus* (Gingerich, 1994), reported from the W5 interval of the Clark's Fork Basin, also fits the *H. minor* size range—with concurrent restriction of the molar talonid that confirms a possible relationship with *H. loomisi* (see below).

Hyopsodus minor is very different from earliest Bridgerian *Hyopsodus minusculus* and *Hyopsodus paulus–wortmani,* which are somewhat similar in size. *Hyopsodus minusculus* possesses shared/derived characters in common with *H. paulus–paulus* and *H. paulus–wortmani* and has shorter, less molariform lower premolars than *H. minor. Hyopsodus minor* is biostratigraphically separated from *H. minusculus* in the Wind River Basin (and other basins with a good middle to late Wasatchian record) and does not occur in Lostcabinian horizons, with the exception of CM loc. 936. It does not occur with *H. powellianus–walcottianus* or *H. paulus–paulus.*

Hyopsodus minor is tentatively reported from ?early Lostcabinian CM loc. 936. This marks its only lithosympatric occurrence with *Lambdotherium.* The specimens (CM 40692, 45934, 45938), with poorly differentiated M_2 entoconids and small M_3 hypoconulid, are closer to *H. minor* than to *H. paulus–wortmani* or *H. minusculus.*

The relationships of this poorly known taxon are unclear. With *Hyopsodus loomisi, H. minor* shares small size, a small and posterolabially situated entoconid associated with an indistinct hypoconulid on M_{1-2}, relatively open molar talonids, small upper molar hypocones, and low, conical cusps on all teeth. If these similarities imply close relationship, then in parallel with changes in the *Hyopsodus paulus* lineage, the "*Hyopsodus loomisi/minor*" transition involved the gradual acquisition of relatively larger third molars and more strongly expressed anterior and labial cingula. Gingerich (1974*a*) has given stratophenetic evidence for a small *Hyopsodus* lineage from the Lysite beds of the Willwood Formation that agrees in size with *Hyopsodus minor* from the Wind River Basin. Alternatively, *Hyopsodus minor* may have had a southern origin completely independent from the Bighorn Basin. Two very small jaws (CM 45976 and CM 60585) from the San Juan Basin Almagre and Largo are similar in molar talonid morphology to *Hyopsodus minor.* Although these specimens are too fragmentary to refer to a new species, they alternatively may represent a new taxon because of their extremely small size (see Fig. 23). Other referred San Juan Basin material is nearly identical to specimens from the Piceance Basin. As mentioned above, *H. minor* is well represented in late Graybullian/early Lysitean levels of the DeBeque Formation of the Piceance Basin.

Hyopsodus loomisi McKenna, 1960
(Fig. 13, 16; Table 7)

Holotype.—UCMP 44781. $RP^2–M^2$. Collected from beds near Four Mile Creek, Washakie Basin, Colorado.

Emended Diagnosis.—Smaller than other *Hyopsodus.* In contrast to other *Hyopsodus,* transverse width of M^1 equal to or only slightly wider than P^4. In contrast to *H. paulus–simplex,* labial cingula of premolars and molars very weak or absent, especially in area basal to the cusps (premolar paracone, molar paracone and metacone); anterior cingula of molars weak and not at all anteriorly expanded. M^3 smaller than in all other *Hyopsodus.* Hypocone on M^{1-2} labially situated and not as distinctly separated from protocone as in *Hyopsodus paulus* and larger *Hyopsodus* lineages. Cusps of lower dentition lower crowned and premolars shorter than in *H. paulus–simplex.* Entoconid labially situated, in contrast to other *Hyopsodus* except some *H. minor,* talonid width equal to or less than trigonid width. M_3 very short, posterior cusps often not as separate as those of *H. paulus–simplex.* Paraconid more frequent on trigonid of M_{1-3} than in all other North American *Hyopsodus.*

Diagnostic Series.—UCMP 44781 (type, *Hyopsodus loomisi*). CM 12375, 16751, 51984, 53715, 53893, 57989, 58104.

Referred Specimens.—CM 6428, 11460–11462, 12110, 12121, 12149–12150, 12165, 12171, 12241, 12243, 12262, 12274, 12298, 12346, 12354, 12361, 12363, ?12364, 12375, 12380, 12383, 12385, 12387–12388, 12415, 12417, 16751, 16990, 28998, 34315 (in part), 34403, 36121, 36123–36126, 36128, ?36130, 36132, 36145, 36151, 36222–36223, 36228, 36232, 36234, ?36238, 36240–36242, 36244–36245, 36247, 36249, 36251, 36552, ?36553, 36616, 36621, 36625, 36627, 36712, 36715, ?36719, 36722, 36724–36727, 36732, 36734, ?36736, 36737–36739, 36741, 36747, ?36748, ?36753, 36755, 36757–36761, 37370, 39428 (in part), 39429 (in part), 39430 (in part), 39432 (in part), 39454, 39455 (in part), 39456 (in part), 39461, 39463 (in part), 51983–51984, 51986, 51990–51991, 51993, 53704–53707, 53711–53712, 53715, 53717–53720, 53725, 57957, 57959–57960, ?57962, 57964, 57989–57990, 58085, 58087, 58099, 58102–58106, ?58108, 58211–58212, 58216, ?58218, 58219. ACM 6239, 10096. UC 44781 (type, *H. loomisi*), referred specimens in McKenna, 1960. (Elk Creek

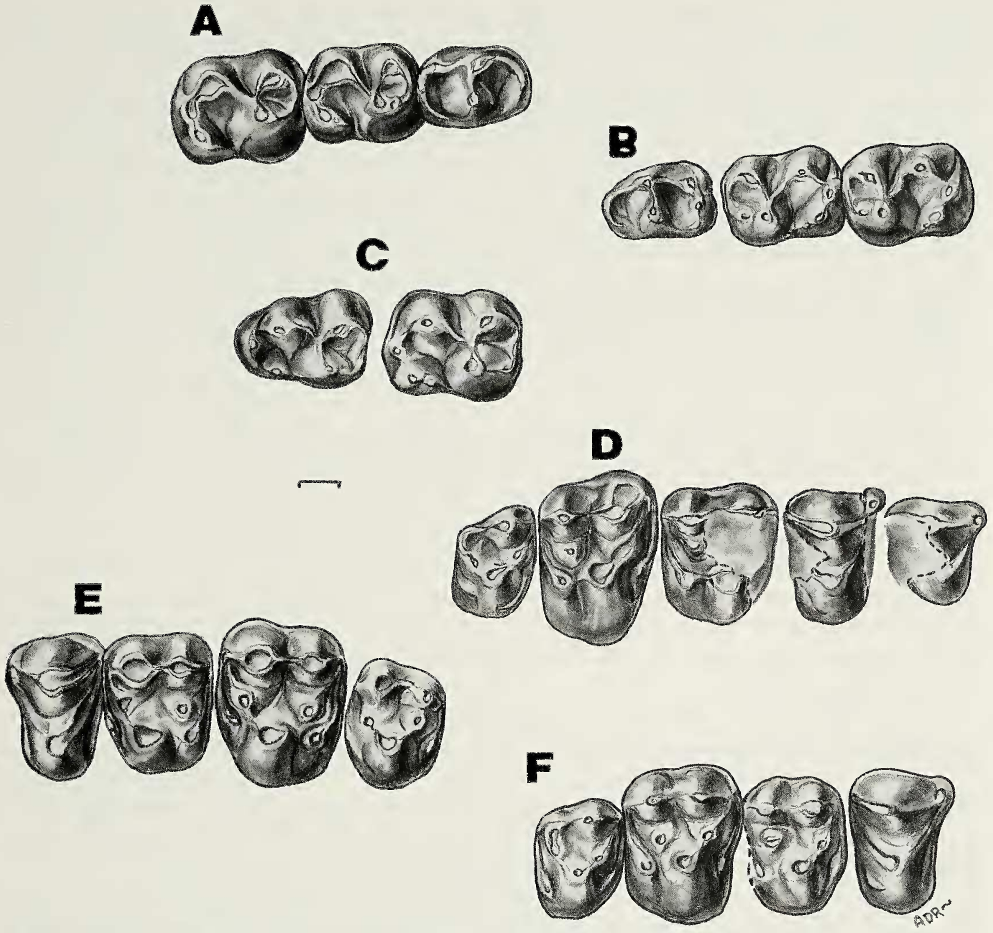

Fig. 16.—Specimens of *Hyopsodus loomisi.* A, CM 51993; B, CM 51984; C, CM 36616; D, CM 53715; E, CM 16751 (left); F, CM 12375. Scale equals 1 mm.

facies, Willwood Fm., tentatively referred). Referred specimens of *Hyopsodus* sp. nov. (Bown, 1979: 102).

Localities.—CM 140–157, 873, 953, Dorsey Creek loc. "*H.* sp. nov. localities" of Bown, 1979. UCMP West Alheit Pocket loc. (McKenna, 1960; partly equals CM loc. 953).

Known Distribution.—Sandcouleean through ?mid-Graybullian of Bighorn and Clark's Fork basins, Wyoming; earliest Eocene of Wasatch Formation, Washakie Basin, northwestern Colorado.

Discussion.—The portion of the diagnosis concerning the upper dentition of *Hyopsodus loomisi* is essentially unchanged from that of McKenna (1960). Lower molar characters have been added to the diagnosis here. McKenna concluded that lower molar attributes were of no value in discriminating *Hyopsodus loomisi* from *H. miticulus* (= *H. paulus–simplex* here), and discounted Denison's (1937) remarks concerning differing molar proportions between two possible species. Although the statement "differs in the proportions of the molars" (Denison, 1937:

Table 7.—Summary of statistics, lower and upper dentitions of *Hyopsodus loomisi*. High, low, mean, SD in mm.

	P_3 (L, W)	P_4 (L, W)	M_1 (L, W)	M_2 (L, W)	M_3 (L, W)
High	3.0, 2.2	3.4, 2.5	3.9, 3.2	4.0, 3.5	4.1, 3.0
Low	2.5, 1.9	3.0, 2.2	3.3, 2.6	3.5, 2.9	3.4, 2.5
n	5	21	49	62	43
Mean	2.7, 2.1	3.2, 2.4	3.5, 2.9	3.8, 3.2	3.8, 2.8
SD	0.19, 0.10	0.10, 0.10	0.11, 0.14	0.12, 0.15	0.18, 0.14
CV	7.0, 4.8	3.1, 4.2	3.1, 4.8	3.2, 4.7	4.7, 5.0
	P^3 (L, W)	P^4 (L, W)	M^1 (L, W)	M^2 (L, W)	M^3 (L, W)
High	3.0, 3.0	3.4, 4.3	3.6, 4.7	3.9, 5.8	3.0, 3.9
Low	— —	2.9, 3.9	3.1, 3.6	3.4, 4.5	2.5, 3.3
n	1	10	21	17	17
Mean	— —	3.1, 4.1	3.3, 4.2	3.7, 5.0	2.6, 3.5
SD	— —	0.14, 0.10	0.15, 0.21	0.16, .0.31	0.15, 0.14
CV	— —	4.5, 2.4	4.5, 5.0	4.3, 6.2	5.8, 4.0

12; citation from McKenna, 1960) is quite vague, two lower molar phena, partly correlated with bimodal size distributions at some localities, are discernible at Sandcouleean and Graybullian localities. Examples include CM 36616 (*H. loomisi*) and CM 57991 (*H. paulus–simplex*) from CM loc. 873, which, although similar in lower molar size, are as dentally distinct as the diagnoses of *H. loomisi* and *H. paulus–simplex*.

Hyopsodus loomisi probably includes Bown's (1979) *Hyopsodus* sp. nov. from the Sand Creek facies of the lower Willwood Formation. Bown mentions shared characters, and the figured specimen is similar to *H. loomisi* in its poorly developed ectocingula, relatively small overall size, and weak, labially situated hypocone on M^{1-2}. These Bighorn Basin specimens of *H. loomisi* are tentatively referred here, as they were not examined firsthand.

Graybullian specimens referred to *Hyopsodus loomisi* differ from those from Four Mile (McKenna, 1960) in smaller average size and perhaps more nearly square M^{1-2}. Within the Graybullian, *H. loomisi* from CM loc. 873 is larger than that from other CM localities and shows a generally better developed paraconid on M_{1-3}. Stage of evolution in *Hyopsodus loomisi* may account for such differences (and similar differences in the other Wasatchian lineages). Progressively smaller size in *H. loomisi* from successively younger strata is inferred as the norm for this species, but specimens referred to *H. loomisi* exhibit a normal morphologic distribution of the diagnostic characters.

The temporal duration of *H. loomisi* is not precisely known due to a lack of stratigraphic control or coverage for the CM Graybullian specimens. Specimens meeting the diagnostic criteria of this species are recognized at Graybullian CM localities 873, 953, Dorsey Creek, the localities of J. L. Kay (CM), and Elk Creek. If the change in morphology of *Hyopsodus loomisi* proceeded at the same rate as the size divergence noted in the Willwood Formation (Gingerich, 1974*a*; results of this study, see discussion of *H. paulus–simplex*), then *H. loomisi* may be inferred to span most, if not all, of the Graybullian Land Mammal Subage. There are specimens of *Hyopsodus minor* in the CM Graybullian collections, but *H. minor* never occurs with *Hyopsodus loomisi* at the same locality. Small-sized *Hyopsodus* specimens from the University of Michigan, Yale, and USGS collections, not examined here, may document the pattern of anagenetic change and geologic range of both taxa. Similarly, analysis of Graybullian *H. paulus* from these collections should improve the systematic resolution of *H. paulus–simplex.*

As mentioned previously, *H. loomisi* may be closely related to *Hyopsodus minor.* Lysitean *Hyopsodus minor,* other than being smaller in size, is very close to small *Hyopsodus* from the Piceance and San Juan basins. Together they may comprise a sister group to the more northerly *Hyopsodus loomisi.* Outside of the Bighorn Basin, the Graybullian/Lysitean transition is incompletely known, making hypotheses contrasting cladogenesis, anagenesis, and immigration difficult to assess. More recent faunal analyses of the Willwood Formation (Schankler, 1980; Badgley, 1990; Bown and Beard, 1990) have treated *H. minor* and *H.* "*loomisi/latidens*" (of Gingerich, 1974*a*) as representative of the same lineage (see Badgley, 1990:165, table 8). As mentioned above, Gingerich's (1994) *Hyopsodus pauxillus* seems to bridge this gap nicely. These conclusions need further interbasinal correlation for support.

Hyopsodus loomisi, as a discrete morph different from *H. minor,* is limited to the Bighorn/Clark's Fork Basin area (aside from the Four Mile localities of Colorado) and does not persist beyond the Graybullian of western North America.

Hyopsodus powellianus Cope, 1884

Hyopsodus browni Loomis, 1905.
Hyopsodus jacksoni Loomis, 1905.
Hyopsodus lawsoni Loomis, 1905.
Hyopsodus powellianus browni Matthew, 1915*b.*
Hyopsodus walcottianus Matthew, 1915*b.*

Holotype.—AMNH 4147, RM_{1-3}. Collected from the Willwood Formation, Bighorn Basin, Wyoming.

Included Lineage Segments.—Hyopsodus powellianus–powellianus, H. powellianus–walcottianus.

Diagnosis.—Larger than other *Hyopsodus*; lineage segment *H. powellianus–walcottianus* is largest known *Hyopsodus.* Length of P^3 approaches or exceeds width and crown is more triangular than in other *Hyopsodus.* Anterior cingula on upper molars, and to a lesser extent on P^4, broader and more anteriorly expanded than in other *Hyopsodus.* In contrast to *H. paulus,* M^3 hypocingula strongly developed and distinctly arcuate, often flares posteriorly; metacone strong but lingually placed in comparison to *H. paulus.* Labial ribs on upper dentition better developed than in *H. minor* and *H. loomisi.* M_{1-2} hypoconulid larger than in other *Hyopsodus,* with inflated base; molar talonids are more incised than basined. Unlike other *Hyopsodus,* interior talonid margins dominated by inflation of talonid cusps. Unlike other *Hyopsodus* other than *H. paulus–lysitensis,* posthypocristid on P_4 strongly developed, often enclosing most of lingual part of talonid basin. Talonid of P_4 comparatively longer than in other *Hyopsodus,* and very rarely notched. Molar paralophid stronger and somewhat more elevated than in other *Hyopsodus*; paraconid usually vestigial, smaller, and structurally does not affect trigonid morphology (as in *H. paulus*). Metastylid as commonly occurring as in *H. paulus,* entostylid more common and comparatively larger.

Referred Specimens.—Listed under individual lineage segments.

Known Distribution.—Lysitean of Buffalo Basin, Wyoming; Lysitean through Lostcabinian of Bighorn Basin, Wyoming; Lysitean through earliest Bridgerian of Wind River Basin, Wyoming; late Graybullian/early Lysitean of Piceance Basin, Colorado.

Discussion.—Like *H. paulus, Hyopsodus powellianus* appears to be an anagenetically evolving lineage. This conclusion is based primarily on the record preserved in the northeastern Wind River Basin and the Bighorn Basin. Large-sized *Hyopsodus* from the more southern basins are not so easily resolved. Specimens that exhibit the diagnostic features of *Hyopsodus powellianus* (near a Wind River Lysitean grade of morphology, see below) are present at the Scenery Gulch locality in the DeBeque Formation. Kihm (1984) noted a *Hyopsodus powellianus* event (first occurrence) in the DeBeque Formation at a higher level, so the Scenery Gulch specimens appear to contradict his immigration hypothesis.

Material approaching the size range of *H. powellianus* occurs in both levels of the San Jose Formation and in the lower levels of the DeBeque Formation. These specimens will be discussed in more detail below as a separate taxon, *Hyopsodus* sp., cf. *H. mentalis.*

In the Wind River Basin, *H. powellianus* exhibits a pattern of morphologic change through time similar to that of the *Hyopsodus paulus* lineage. It is marked by the gradual evolution of dental traits and canalization of these characters in specimens from successively younger sediments. Anagenetic acquisitions are detailed in the lineage segments of *H. powellianus* and include increase in size. There is no shortening of the lower premolar series; both P_3 and P_4 are comparatively elongate and may increase slightly in relative length through time. The lack of plentiful *H. powellianus–walcottianus* material makes it difficult to assert this with confidence.

The directional increase in absolute tooth size supports the origin of a large-sized *Hyopsodus* lineage noted by Gingerich (1974*a*) in the Graybullian and Lysitean levels of the Willwood Formation. In the Wind River Basin, this pattern continues through the mid-Lysitean–Lostcabinian–Gardnerbuttean Land Mammal Subages, much of which are poorly represented or nonexistent in the Willwood Formation. A Graybullian–Lysitean immigration and/or mixing of taxa between the Wind River and Bighorn basins is certainly a strong possibility (discussed below in more detail).

Taxonomic difficulties with this large-sized lineage are not so severe as in other Wasatchian *Hyopsodus* for three reasons. First, the lineage, at least from the Lysitean onward, does not appear to give rise to new taxa. Secondly, the species name is based on a holotype (as compared to the types of *H. miticulus* and *H. mentalis*) collected by Cope from a locality in the Bighorn Basin (not geographically and faunally disjunct from other basins). Additionally, the fossil record is far more complete and controlled by biostratigraphy in the case of *Hyopsodus powellianus* as a taxonomic concept contrasted to that of *H. miticulus* and *H. mentalis* from the San Juan Basin.

Hyopsodus powellianus extends from the Lysitean (Gingerich's [1974*a*] Bighorn Basin data suggests very probably earlier) through the Lostcabinian of the Wind River Basin and includes *Hyopsodus walcottianus.* It co-occurs with *Hyopsodus paulus–lysitensis* and *Hyopsodus minor* in the Lysitean, and *Hyopsodus paulus–wortmani* in the Lostcabinian. According to Stucky (1982, 1984*a*, 1984*b*), one of the extinctions marking the close of the Lostcabinian was that of *H. walcottianus.* Since 1984, one well-preserved associated dentition of "*H walcottianus*" (*Hyopsodus powellianus–walcottianus* here) has been recovered from the Gardnerbuttean of the Wind River Basin high in the horizons of CM loc. 34. The

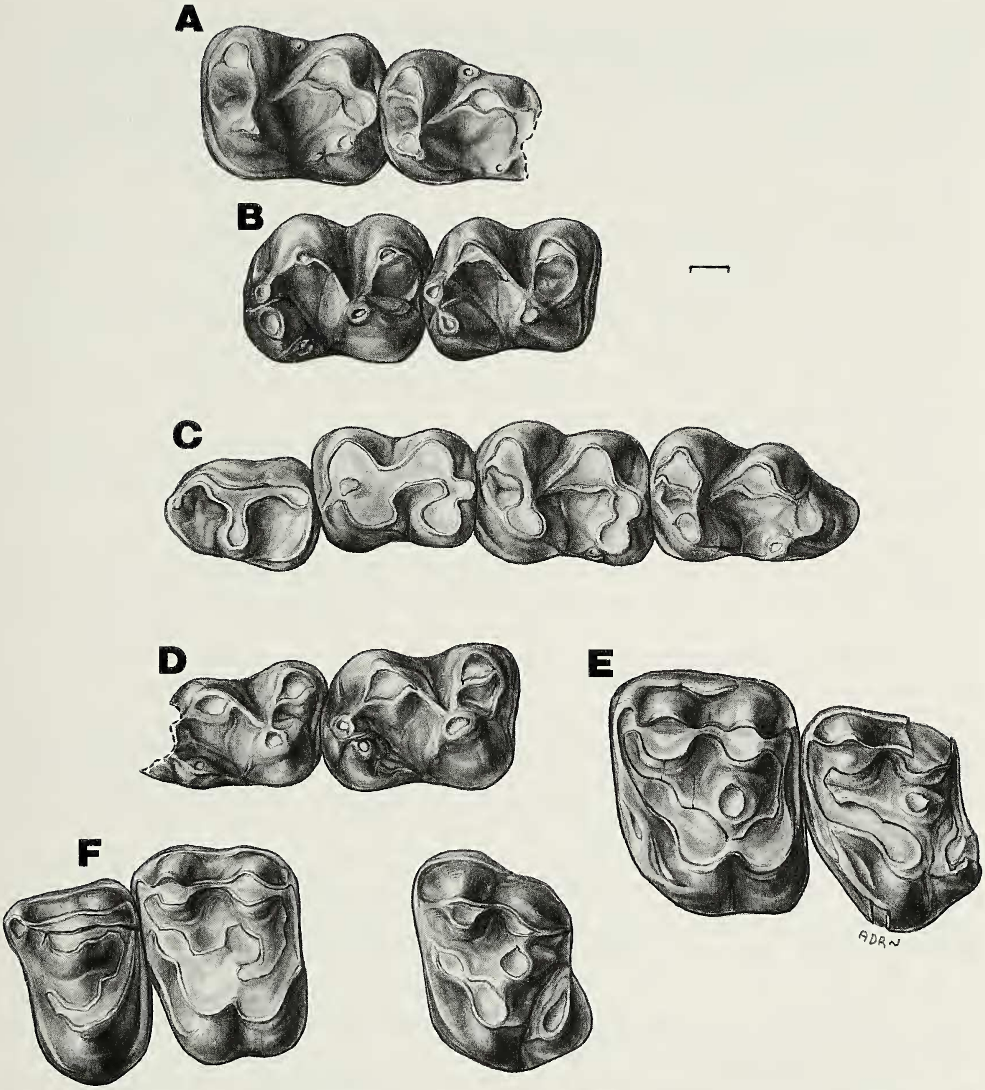

Fig. 17.—Specimens of *Hyopsodus powellianus–walcottianus.* A, CM 45257; B, CM 40668; C, CM 45158 (lower); D, CM 45232; E, CM 40667; F, CM 45158 (upper). Scale equals 1 mm.

biostratigraphic range of this lineage is here formally extended into the earliest Bridgerian.

Lineage Segment *Hyopsodus powellianus–walcottianus*
(Fig. 6, 7, 8, 17; Tables 8, 9)

Diagnosis.—Largest *Hyopsodus* (mean length of lower M_2, 6.5 mm). More inflated cusps on all molars and premolars. Entostylid on M_{1-3} robust and more common than in all other *Hyopsodus.* Differs from *H. powellianus–powellianus* in having M_{1-2} hypoconulids larger, incompletely separated from entoconids, aligned with entoconids, and large entostylids in plane oblique to anteroposterior axis of molars. Lower molar metaconids comparatively larger than in other early Eocene *Hyopsodus,* paraconids most completely absent in *Hyopsodus*; trigonids more anteroposteriorly compressed. Protoconids more anteriorly placed relative to metaconids than in *H. paulus.* Anterior cingula of upper molars more expanded than in other *Hyopsodus,* particularly in the area immediately anterior to protocone. M^3 comparatively larger than in lineage segment *H. powellianus–powellianus.*

Diagnostic Series.—AMNH 14654 (type, *Hyopsodus walcottianus*), 55247. CM 40667, 45158, 45232.

Referred Specimens.—CM 21220 (in part), 22337–22338, 40667–40668, 45155, 45158, 45232, 45257, 45263, 46472, 49451. AMNH 14654 (type, *H. walcottianus*), 55247.

Localities.—CM 34, 91, 216, 1039, 1040, 1046, Kay's Lost Cabin SE of Riverton loc. AMNH Lost Cabin beds.

Known Distribution.—Lostcabinian through Gardnerbuttean of Wind River Basin, Wyoming. Lostcabinian of Bighorn and Green River basins, Wyoming; Huerfano Basin, Colorado.

Discussion.—*Hyopsodus powellianus–walcottianus* is the largest known taxon of *Hyopsodus* (larger than *H. sholemi* of Krishtalka, 1979) and, in the late Wasatchian, may have been ecologically competitive with such herbivores as *Phenacodus vortmani* and *Hyracotherium vassacciense.* However, it is decidedly more rare than either of these taxa in the Wind River Basin. Paleoecologic and taphonomic considerations of Wind River Formation sediments will be discussed in a subsequent section of this report. If *H. powellianus–walcottianus* was a larger herbivore occupying a different niche than smaller, penecontemporaneous lineages of *Hyopsodus,* it is not reflected in the morphology of the known tarsal and limb elements, part of AMNH 14654, described and figured by Matthew (1915*b*). They differ from *H. paulus* in size only.

Overall, the dentition of *Hyopsodus powellianus–walcottianus* is quite different from that in other species of *Hyopsodus.* Lower molars especially differ in their talonid cusps. The typical morphology includes a quite enlarged entostylid ("cusp-sized" on some specimens such as CM 40668). The entostylid and the entoconid are low crowned and swollen with bases closely appressed. On some specimens, only a shallow groove separates the hypoconulid from the entoconid, which is subequal in size to the hypoconulid.

The range in variation of this lineage segment encompasses specimens such as CM 40668 (above) as well as other specimens (e.g., CM 45257) that, although as large as CM 40668, are not quite as bunodont and somewhat closer to some specimens of *Hyopsodus powellianus–powellianus.* This pattern closely approximates that in temporally successive lineage segments of *Hyopsodus paulus.* Other variable characters are: size of lower molar metaconids; angle of the hypoconulid/entoconid cusp plane in relation to the long axis of the tooth; and external cingula on the upper teeth, which can be quite wide and bear cuspules. As in *H. paulus,* the heel of M_3 in the *Hyopsodus powellianus* lineage becomes more distinct and posteriorly extended through time. This is indicated by the longer M_3 of Lostcabinian *H. powellianus–walcottianus* compared to Lysitean *H. powellianus–powellianus.*

AMNH specimens from the Lostcabinian level of the Huerfano Basin (AMNH 55247 is referred here) appear to be smaller in overall molar size. Aside from somewhat smaller size, these specimens fit the morphologic diagnosis of *Hyop-*

Table 8.—Summary of statistics, lower dentitions of *Hyopsodua powellianus* (lineage segments *H. powellianus–walcottianus, H. powellianus–powellianus*). High, low, mean, SD in mm.

	P_3 (L, W)	P_4 (L, W)	M_1 (L, W)	M_2 (L, W)	M_3 (L, W)
H. powellianus–walcottianus					
High	4.8, 3.2	5.5, 4.1	6.4, 4.9	6.5, 5.7	7.8, 5.0
Low	3.8, 2.4	4.7, 3.6	6.0, 4.6	6.4, 5.3	7.2, 4.9
n	2	3	2	4	2
Mean	4.3, 2.8	5.1, 3.8	6.2, 4.8	6.5, 5.5	7.5, 5.0
SD	— —	0.33, 0.22	— —	0.04, 0.15	— —
CV	— —	6.5, 5.8	— —	0.6, 2.7	— —
H. powellianus–powellianus					
High	4.5, 2.8	4.9, 3.6	5.7, 4.5	6.2, 5.3	6.8, 4.7
Low	3.7, 2.4	4.1, 2.8	4.8, 3.6	4.9, 3.9	5.1, 3.4
n	23	79	134	175	159
Mean	4.2, 2.6	4.5, 3.2	5.1, 4.1	5.4, 4.6	5.8, 4.0
SD	0.22, 0.12	0.20, 0.17	0.21, 0.23	0.26, 0.28	0.38, 0.23
CV	5.2, 4.6	4.4, 5.3	4.1, 5.6	4.8, 6.1	6.6, 5.8

sodus powellianus–walcottianus. Hyopsodus powellianus–walcottianus is, so far, unknown from the Gardnerbuttean of the Huerfano.

Lineage Segment *Hyopsodus powellianus–powellianus*
(Fig. 10, 11, 18; Tables 8, 9)

Diagnosis.—Larger than most *Hyopsodus* (mean length of M_2 in Wind River Basin, 5.4 mm). Differs from smaller *Hyopsodus* in having large, conical, not compressed or crescentic, cusps on all molars. Less crescentic protocones on P^{3-4} than in *H. paulus.* Hypocone and associated hypocrista of M^3 well developed, but differs from other *Hyopsodus* in expanding only in area posterolingual to protocone. Parastyle on P^{3-4} more distinct from paracone than in other *Hyopsodus* species, less anteriorly placed than in *H. powellianus–walcottianus.* P^4 usually more quadrate than in penecontemporaneous *Hyopsodus.* Upper molar anterior

Table 9.—Summary of statistics, upper dentitions of *Hyopsodus powellianus* (lineage segments *H. powellianus–walcottianus, H. powellianus–powellianus*). High, low, mean, SD in mm.

	P^3 (L, W)	P^4 (L, W)	M^1 (L, W)	M^2 (L, W)	M^3 (L, W)
H. powellianus–walcottianus					
High	— —	4.9, 6.5	5.6, 7.6	6.7, 8.5	5.8, 7.5
Low	— —	4.3, 6.1	— —	— —	5.3, 7.5
n	-	2	1	1	2
Mean	— —	4.6, 6.3	— —	— —	5.6, 7.5
SD	— —	— —	— —	— —	— —
CV	— —	— —	— —	— —	— —
H. powellianus–powellianus					
High	4.5, 4.8	4.5, 5.7	5.2, 6.6	6.1, 7.7	5.1, 6.5
Low	3.7, 3.7	3.6, 4.6	4.5, 5.6	4.6, 6.1	3.8, 5.2
n	20	35	37	50	43
Mean	4.1, 4.1	4.1, 5.2	4.9, 6.1	5.2, 7.1	4.2, 5.8
SD	0.23, 0.27	0.17, 0.24	0.16, 0.28	0.29, 0.40	0.26, 0.34
CV	5.6, 6.6	4.1, 4.6	3.3, 4.6	5.6, 5.6	6.2, 5.9

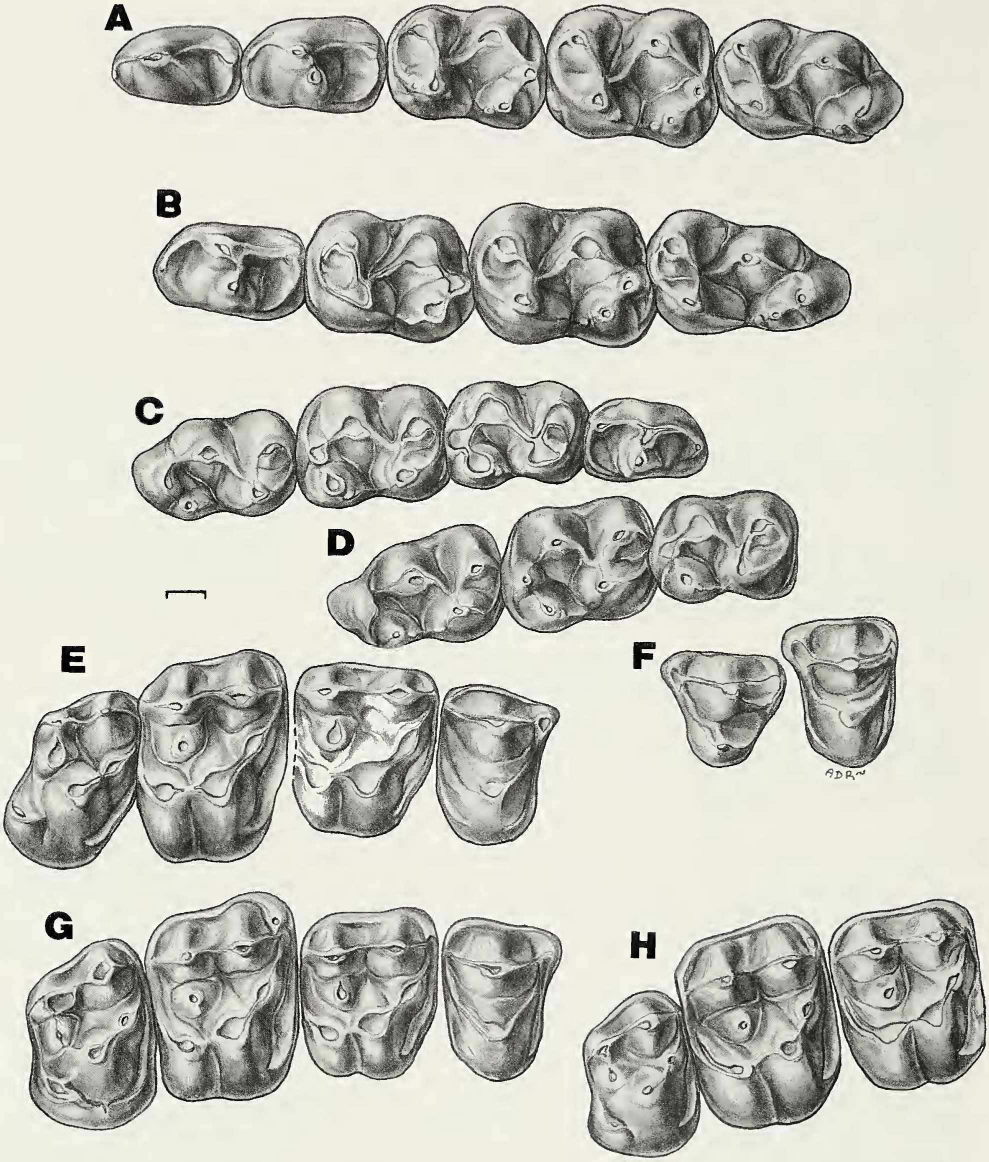

Fig. 18.—Specimens of *Hyopsodus powellianus–powellianus.* A, CM 53829; B, CM 39975; C, CM 19834; D, CM 39790; E, CM 22729; F, CM 54191; G, CM 39508; H, CM 35893. Scale equals 1 mm.

cingula stronger than in *H. paulus,* but not as lingually prominent as in *H. powellianus–walcottianus.* Lower premolar paraconids more anteriorly placed on most specimens than in *Hyopsodus paulus–lysitensis* and *H. minor.* Differs from other *Hyopsodus* (except *H. powellianus–walcottianus,* which further exaggerates these features) in: lower molar metaconid large and tall, and metastylid variable. Paraconid very infrequent and always small, if present. Molar trigonids more anteroposteriorly compressed than penecontemporaneous *Hyopsodus.* M_{1-2} hypoconulid and entoconid enlarged, close to one another on most specimens; entostylid common. Hypoconulid lobe of M_3 very large and well separated from entoconid.

Diagnostic Series.—AMNH 4147 (type, *Hyopsodus powellianus*). ACM 3232 (type, *Hyopsodus browni*). CM 4915, 19834, 22729, 39139, 39167, 39168, 39759, 39975, 53829.

Referred Specimens.—CM 4915, 9924, 15781, 19809–19810, 19812–19815, 19816, 19817, 19820–19822, 19824, 19826, 19832, 19834–19835, 19838, 19840, 19842–19847, 19849, 19851 (in part), 19868, 19880, 20877, 20882, 20890, 20919, 20926, 20943 (in part), 21795–21796, 21891–21892, 21900, 21905–21906, 21911–21912, 21916, 22705–22706, 22711, 22714, 22716, 22718 (in part), 22721–22724, 22727, 22729–22732, 22734 (in part), 22735 (in part), 22736 (in part), 28650–28651, 28656, 28664, 28666, 28667 (in part), 28668 (in part), 28670 (in part), 28671 (in part), 28672 (in part), 28729–28730, 28732, 28734–28736, 28749–28751, 28757–28758, 28760, 28762–28763, 28765, 28767–28769, 28771–28773, 28774 (in part), 28775–28776, 28777 (in part), 28778, 28792–28794, 28936 (in part), 29186–29190, 29196 (in part), 34477, 35887–35888, 35890, 35892, 35894–35895, 35898–35899, 35900–35903, 35906, 35908, 35961, 36069–36070, 36072 (in part), 36072–36073, 36100 (in part), 36101 (in part), 36102 (in part), 36103 (in part), 37057 (in part), 37058, 37059 (in part), 37060 (in part), 37067, 37069 (in part), 37070, 37071 (in part), 39139, 39141–39147, 39149–39152, 39153–39157, 39159, 39165–39168, 39170, 39173–39174, 39177, 39179–39180, 39184, 39188–39189, 39191, 39193, 39214–39216, 39232, 39234, 39229, 39236, 39242–39243, 39278, 39284–39285, 39287–39288, 39292, 39470, 39499, 39501–39503, 39505–39508, 39518 (in part), 39520–39525, 39527–39528, 39530, 39532–39535, 39536–39539, 39541–39542, 39544–39547, 39549, 39551–39557, 39558, 39560–39562, 39564–39566, 39568, 39570 (in part), 39571, 39573–39575, 39661–39662, 39664–39666, 39672, 39750–39751, 39757, 39759–39760, 39789 (in part), 39791, 39795–39797, 39798 (in part), 39802, 39806–39811, 39813, ?39816, 39818, 39821 (in part), 39824 (in part), 39826–39829, 39831–39833, 39836, 39839, 39842–39847, 39849, 39851, 39853–39856, 39858–39860, 39861 (in part), 39862, 39864, 39866–39870, 39897, ?39900, 39931, 39973–39976, 39980 (in part), 45306, 45308, 45312, 45316–45317, 45319–45320, 45331, 45336–45338, 45343, 45346, 45349, 45352, 45356, 45364–45365, 45367–45369, 45372, 45374, ?45377, ?45378, 45380, 45383 (in part), 45385–45387, 45392–45395, 45397–45399, 45901, 45907, 45909–45911, 45913, 45916–45917, 45919, 45922, 45927, 46427, 46473–46474, 46477, 46480–46481, 46484–46485, 46487–46490, 46499, 46592, 47262, 47266–47268, 49401–49403, 49405–49407, 49409–49410, 49412–49414, 49417–49420, 49423–49424, 49480–49481, 49484–49485, 49488, 49491–49499, 53795–53796, 53798, 53800, 53802, 53806, 53809–53810, 53812–53815, 53818–53821, 53823, 53825–53826, 53829, 53831, 53833, 54095–54096, 54100, 54108–54110, 54112–54115, 54117–54118, 54120–54121, 54174–54175, 54179–54182, 54185–54187, 54191, 54194–54196, 54198, 54201–54202, 60199–60201, 60203–60205. AMNH 4147 (type, *H. powellianus*), 15015, 15613–15614, 15616. ACM 3232 (type, "*H. browni*"), 3246 (type, "*H. jacksoni*").

Localities.—CM 111–112, 114, 118, 130, 793–794, 797, 800, 801–803, 805–807, 809–813, 877, 927–931, 964–966, 1007–1009, 1064, 1091. ACM Lysite localities. AMNH Bighorn Basin Lysite.

Known Distribution.—Lysitean of Wind River, Bighorn, and Green River basins, Wyoming; Piceance Basin, Colorado.

Discussion.—*Hyopsodus powellianus–powellianus* is extremely common in the Lysite Member of the Wind River Basin where it exceeds *H. paulus–lysitensis* in numbers in most instances.

Measurement data from some localities (Fig. 10, 11) indicate that large specimens of *Hyopsodus* from the Lysite Member, when grouped together, show a higher coefficient of variation and a bimodal distribution in size of M_2. Loomis (1905), noting size and character differences among a limited number of specimens, named four species of large *Hyopsodus* from the Lysite Member. Matthew (1915*b*) synonymized these species as the subspecies *H. powellianus browni.* This indicated that the entire Wind River collection was on average smaller than *Hyopsodus powellianus* from the Bighorn Basin. Kelley and Wood (1954) strengthened these conclusions but abandoned the subspecies *browni.* The Lysitean histograms reported here might also be interpreted as bimodal or even trimodal (Fig. 10, 11) in the length of M_2. However, the coefficients of variation (Tables 8, 9) are not larger than expected of one taxon (absolute values close to the somewhat smaller *Diacodexis secans–secans* of Krishtalka and Stucky, 1985).

Hyopsodus powellianus from the Bighorn Basin is larger in mean size, but the largest specimens from the Wind River Basin approach it in size. Bighorn Basin material of *H. powellianus* is similar in premolar and molar morphology to the Wind River Lysite *H. powellianus–powellianus,* and aside from average size considerations, these forms are virtually identical. Much of the bimodality in this study is correlated with specific localities; for example, specimens from CM loc. 928 and CM loc. 803 are larger. Localities such as CM loc. 806 and CM loc. 931 have slightly bimodal size distributions, but specimens of *Hyopsodus* show an even distribution of characters that are not positively correlated with the size of the specimen. Plots of M_2 length of specimens from individual Lysite Flats localities (Fig. 19) indicate either no change or a slight increase in average size through time. However, no real trend is apparent; CM loc. 118 and CM loc. 797 (Davis Draw) are upsection from the Lysite Flats localities but specimens are on average somewhat smaller, whereas CM Cedar Ridge specimens are also stratigraphically higher and are uniformly larger. It seems at least possible that slightly different-sized populations of upland and lowland *Hyopsodus powellianus* could have occupied the northeastern margin of the basin in Lysitean times, perhaps with periodic immigration of the even larger individuals from the Bighorn Basin area to the north. The cladogenesis of a large taxon more closely related to *Hyopsodus powellianus–walcottianus* may already have occurred by the Lysitean, perhaps in the Bighorn Basin. These small scale "cladogenetic" events, possibly most common in areas of heterogeneous paleoenvironment, may be responsible for the observed evolutionary pattern of many Eocene taxa. Morphologically, the presence of two very similar populations of *Hyopsodus* cannot be documented, except that the ratio of M_2 to M_1 length is usually higher in the smaller Wind River Lysitean specimens. Analysis of Bighorn Basin material might indicate whether or not further distinctions are valid.

Some of the variable characters of *H. powellianus–powellianus* are the size of the common accessory stylids of the lower molars, degree of paraconid expression (it is never prominent), proximity of the entoconid to the hypoconulid, degree of P_{3-4} talonid enclosure and expression of entoconid on the enclosing posthypocristid of P_4, strength and robusticity of premolar and molar paracones, extent of posterior flaring of the hypocrista of M^3, and various aspects of the labial and lingual cingulids associated with the hypoconulid heel of M_3.

Examples illustrating the variability in this *Hyopsodus* lineage include CM 39975 and CM 53829, which approach *H. powellianus–walcottianus* in molar talonid structure, and CM 39759, which has a smaller entoconid and more discretely distinct hypoconulid on M_{1-2}, but otherwise is nearly identical to CM 39975 and CM 53829 in premolar structure and size. It is inferred that many of the diagnostic characters of *H. powellianus–walcottianus* are the result of canalization of structures variably distributed in the biostratigraphically older *H. powellianus–powellianus* lineage segment. This was accompanied by an increase in size if the transition was a within-basin anagenetic event, or a less significant size increase if the immigration of larger individuals from the Bighorn Basin was involved.

The distribution of characters within *Hyopsodus powellianus–powellianus* is

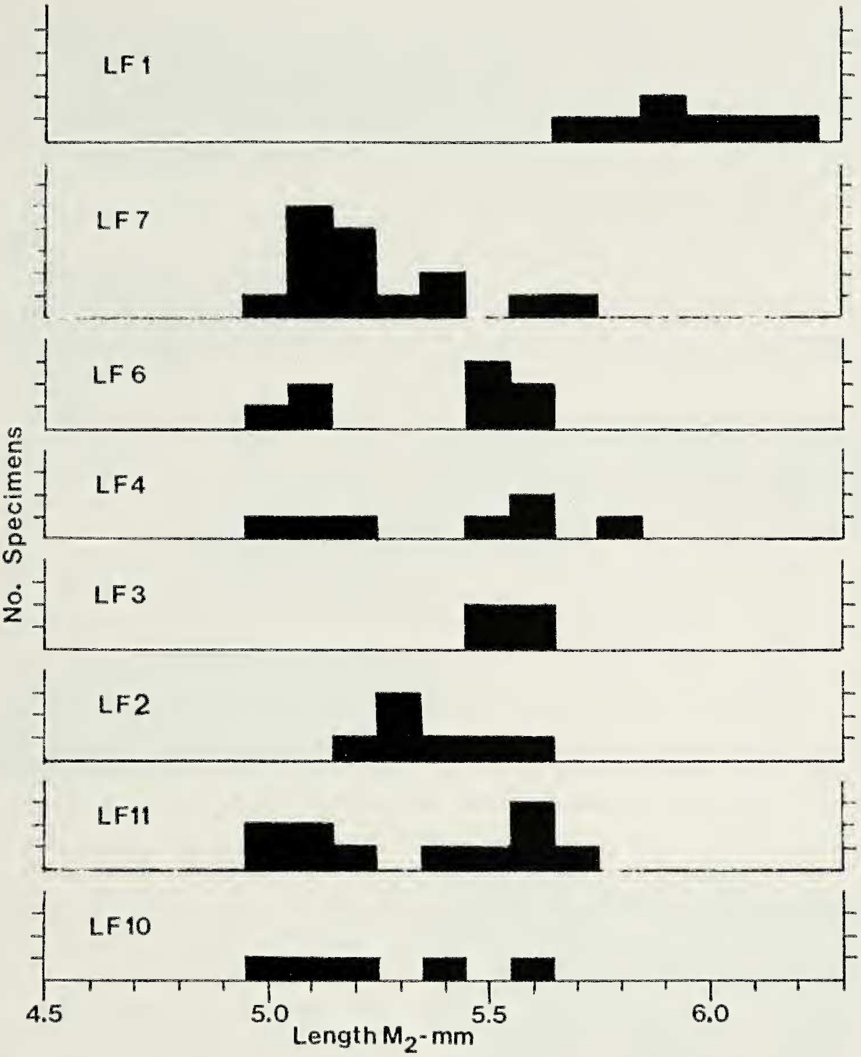

Fig. 19.—Histogram plots of lower second molar lengths of large *Hyopsodus* from Wind River Formation Lysite Flats localities. Localities are positioned in relative stratigraphic order from bottom to top.

noticeably different from that in the other large early Wasatchian form recognized here, *Hyopsodus* sp., cf. *H. mentalis* (below). Isolated upper molars of the two may be difficult to discriminate, but lower premolar and molar trigonid characters as well as a different frequency distribution of molar talonid features seem to distinguish them. These two taxa of *Hyopsodus* do not occur at the same locality, at least in the Wind River Basin.

In the Piceance Basin (Scenery Gulch loc.), one specimen (CM 4915, LP^3–M^3 [Fig. 23]; RP^3–M^2) is very close in morphology (more occlusally triangular P^3; posteriorly splayed hypocingula) to *Hyopsodus powellianus–powellianus* and is assigned to this lineage segment. This specimen is from a locality below the beds designated by Kihm (1984) as marking the first occurrence of the species *H. powellianus.* From this locality, however, other specimens referred here to *H. paulus–lysitensis* may represent the *H.* sp., cf. *H. mentalis* taxon discussed below.

As discussed later in this report, the extreme abundance of *Hyopsodus powellianus–powellianus* compared to the rarely occurring *H. powellianus–walcottianus* may be interesting when viewed from a paleoecological perspective.

Hyopsodus sp., cf. *H. mentalis* (Cope, 1874; Matthew, 1915*b*)
(Fig. 20, 21, 22; Table 10)

(This taxon includes the topotype of *H. mentalis,* some referred *H. mentalis,* the type of *H. lemoinianus* [Cope, 1882*b*] and various material previously referred to *H. powellianus* and *H. miticulus.*)

Diagnosis.—Intermediate in size between *H. paulus* and *H. powellianus,* larger than *H. paulus* lineage at penecontemporaneous localities. P_4 talonid somewhat shorter than *H. powellianus–powellianus*; entoconid much more distinct, hypocristid weaker, does not extend anterolingually to base of metaconid. Molar trigonid not compressed and metaconid less elevated than in *H. powellianus–powellianus,* paraconid more common and larger. Bases of lower molar entoconid and hypoconulid not inflated, cusps usually connected by stronger crest than in most other *Hyopsodus.* Metastylid and entostylid more common than in *H. paulus* and *H. powellianus*; entostylid smaller and more distinct from entoconid base as in *H. paulus,* unlike the cusp-like morphology of *H. powellianus.* Upper molar metacone and paracone less conical, anterior cingula less expanded and hypocone larger and more distinct than in *H. powellianus–powellianus.*

Morphologic Series.—AMNH 4139 (type, *Hyopsodus lemoinianus*), 16194 (topotype, *Hyopsodus mentalis*), 16197. CM 14929, 45946, 46913, 47128, 60565.

Referred Specimens.—(San Jose Formation) CM 14929, 44856, 45983–45985, 45989–45991, 45993, 46862, 46899, 46909, 46913, 46923, 46931, 60564–60566, 60570, 60571, 60572, 60573–60574. AMNH 3307, 16194 (topotype, *H. mentalis*) 16197, 16202, 16304, 86283, 86293. (Wind River, ?early Lysite) CM 45928, 45996 (in part), 45997 (in part), 47011. (Wind River, ?Lysite/?Lost Cabin) CM 34885 (in part), 36451, 40694–40695, 45933, 45936–45937, 45939, 45940–45954, 45957, 45973, 47128, 47912. (Bighorn Basin, Lysite) AMNH 4139 (type, *H. lemoinianus*).

Localities.—CM 858, 936, 1049–1051, 941, 945, 1017–1019, 1021, 1025–1027, 1030–1031, 1033, 1049–1051, 1903–1904, 1907, 1952. AMNH San Juan Basin localities; Bighorn Basin Wasatchian beds (Lysite level).

Known Distribution.—?Late Graybullian/?early Lysitean of San Juan Basin, New Mexico. ?Lysitean of Wind River Basin and Bighorn Basin, Wyoming. ?Late Lysitean/?early Lostcabinian of Wind River Basin, Wyoming.

Discussion.—This is easily the most tenuous grouping of *Hyopsodus* material in this review and should be tested by more detailed comparison of specimens from the San Juan, Bighorn, and Wind River basins. Wind River specimens referred to this taxon show close affinities to the type of *H. lemoinianus* (subsumed in *H. miticulus* by Gazin, 1968) from the Bighorn Basin and large specimens from the Piceance and San Juan basins (probably what Cope intended as *H. mentalis*). Improved biostratigraphic resolution may resolve the relationships of this taxon. Certain primitive but consistent characters and larger size ally the referred specimens for the present time. Its presence as a discrete taxon is indicated by its morphologic distinction from the *Hyopsodus paulus* lineage in the ?early Lysitean of the Wind River Basin at CM localities 1903 and 1904, in the ?early Lostca-

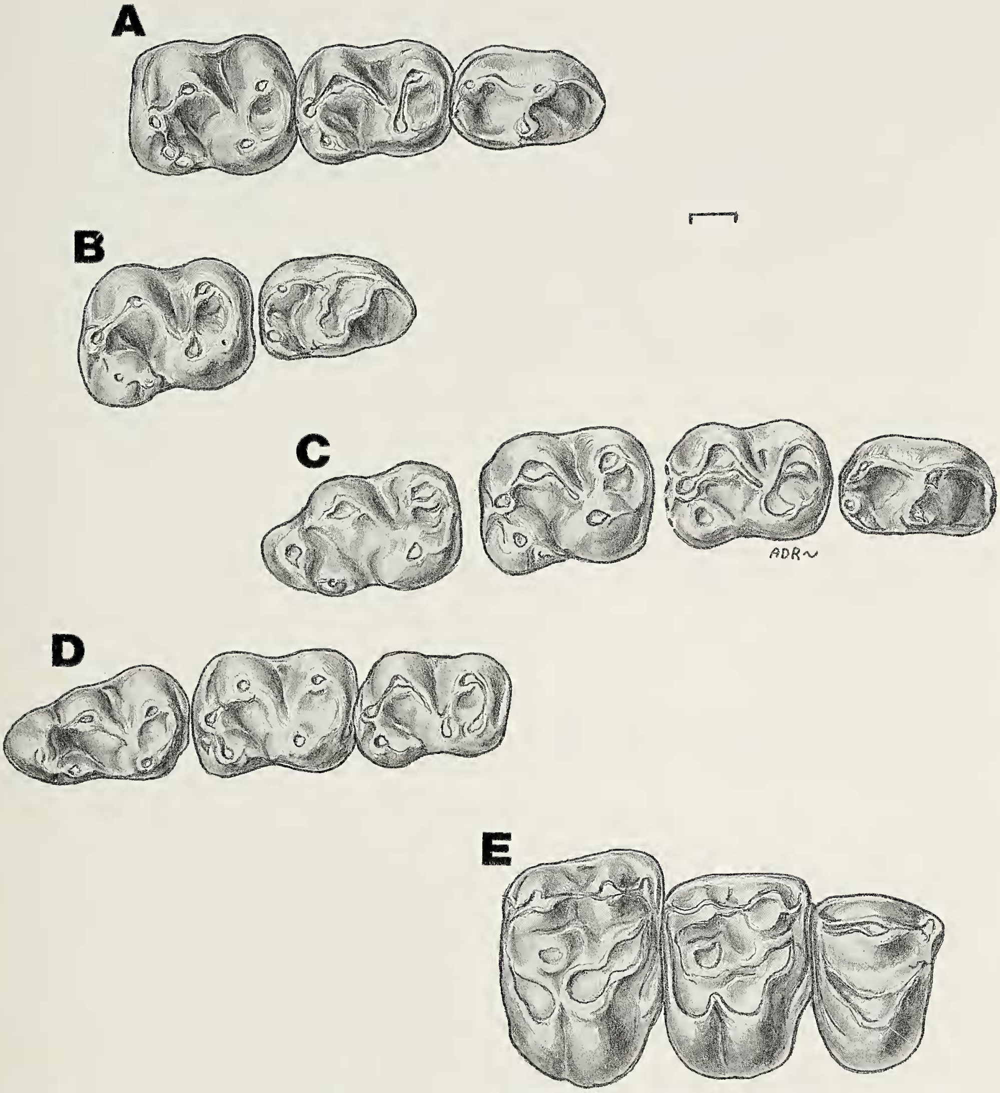

Fig. 20.—Specimens of *Hyopsodus* sp., cf. *H. mentalis*. A, CM 14929; B, CM 47128; C, CM 62663; D, CM 46843; E, CM 62668. Scale equals 1 mm.

binian of the Wind River Basin at CM loc. 1952 and Okie Trail localities, and with "*H miticulus*" (*Hyopsodus paulus–lysitensis*) in the San Juan Basin.

The holotype of *Hyopsodus mentalis,* collected and described by Cope (1875) from the San Juan Basin, was lost at least as early as Matthew's (1915*b*) revision. Matthew designated a topotype from the Largo deposits of the basin and synonymized *H. lemoinianus* (Cope, 1882*a*; AMNH 4139) from the Bighorn Basin with this taxon. Gazin (1968), by synonymizing *Hyopsodus mentalis* with *H. miticulus,* essentially removed this material from systematic consideration. Reexamination of these specimens and the CM San Jose Formation collection has disclosed a number of similarities between the *H. mentalis* topotype and the *H. lemoinianus*

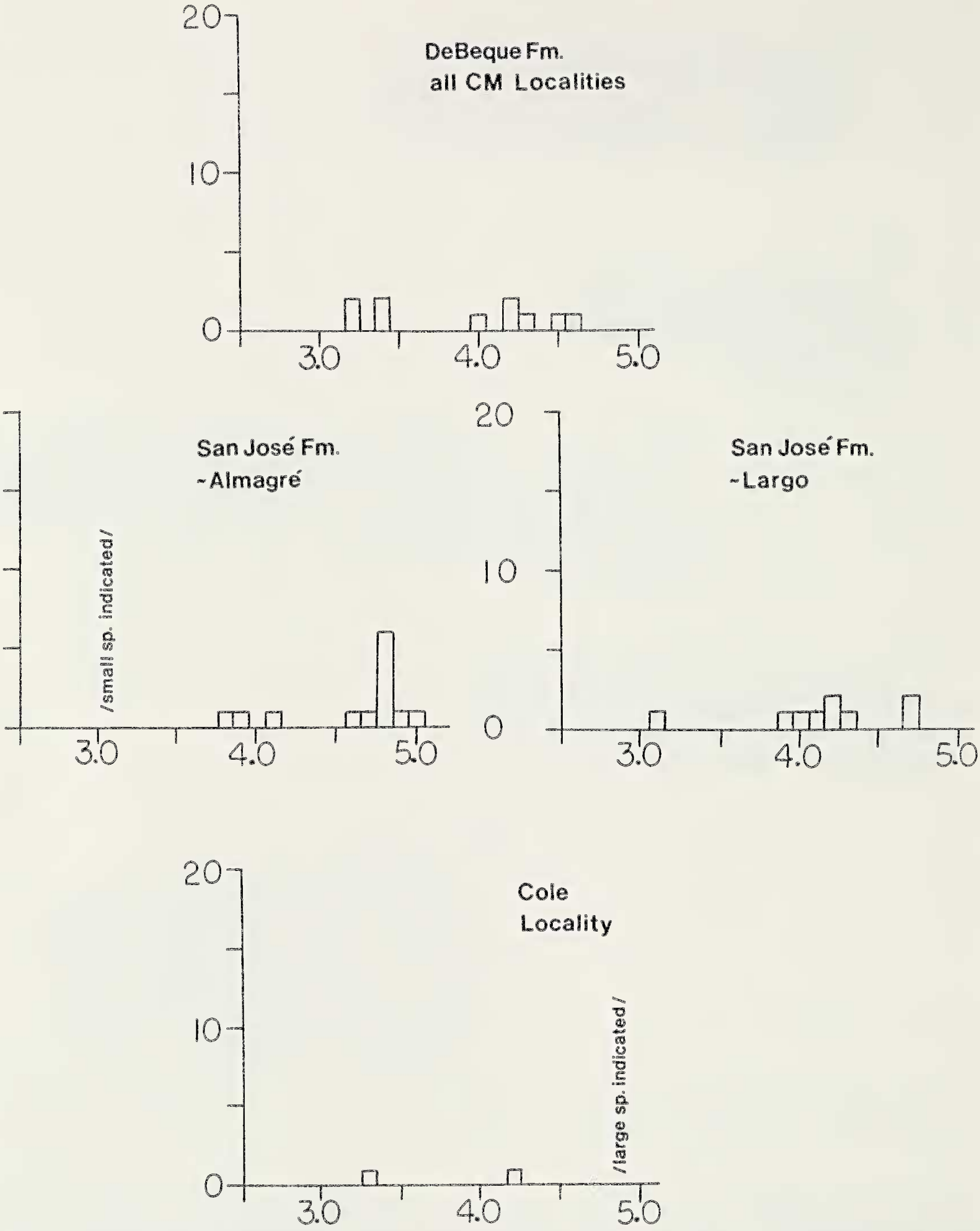

Fig. 21.—Frequency histograms for lower second molars of *Hyopsodus* from ?late Graybullian/?early Lysitean localities from various basins. Cole locality is in the eastern Wind River Basin. Vertical axis, number of individuals; horizontal axis, molar length in mm.

type that are not shared to the same degree by "*Hyopsodus miticulus*" (considered *H. paulus* here). *Hyopsodus lemoinianus* and *H. mentalis* feature more rectangular P_4 and P_3 (but strong entoconid on P_4 of *H. lemoinianus*); a comparatively broader posterior dimension to P_4; larger size of the lower molars, and inflated first and

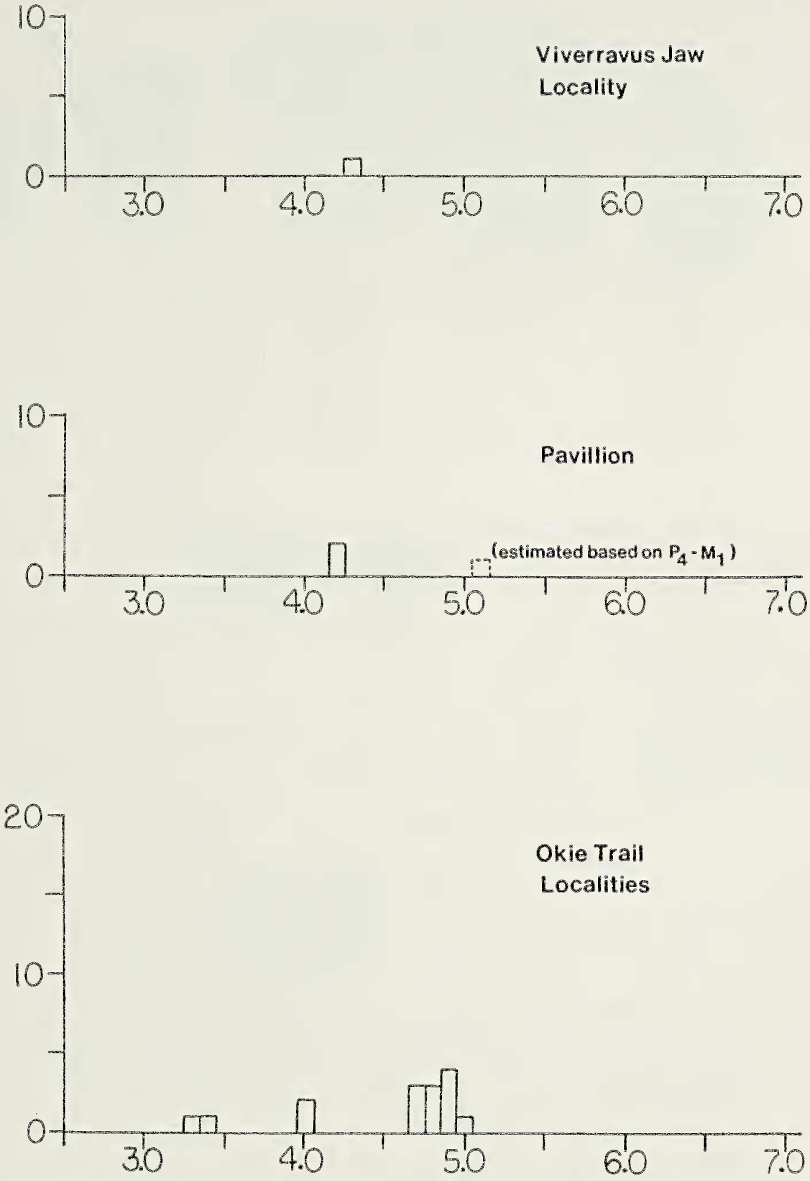

Fig. 22.—Frequency histograms for lower second molars of *Hyopsodus* from ?early Lostcabinian localities in the Wind River Basin. Vertical axis, number of individuals; horizontal axis, molar length in mm.

second molar hypoconulids. *Hyopsodus* sp., cf. *H. mentalis* appears to be intermediate between *Hyopsodus paulus* (M^3 and P^4 morphology, well-separated entoconid/hypoconulid bases) and *Hyopsodus powellianus* in many characters and may be closely related to either of these species.

Hyopsodus sp., cf. *H. mentalis* seems to be absent from the Lysite Member of the Wind River Formation. However, these rocks outcrop only in the immediate

Table 10.—Summary of statistics, lower and upper dentitions of *Hyopsodus* sp., cf. *H. mentalis*. High, low, mean, SD in mm.

	P_3 (L, W)	P_4 (L, W)	M_2 (L, W)	M_2 (L, W0	M_3 (L, W)
High	3.7, 2.5	4.3, 3.3	4.9, 4.1	5.0, 4.5	5.8, 3.5
Low	3.4, 2.4	3.7, 2.7	4.3, 3.3	4.6, 3.9	4.7, 3.3
n	8	19	22	23	17
Mean	3.6, 2.4	4.0, 2.9	4.5, 3.6	4.8, 4.1	5.2, 3.4
SD	0.12, 0.04	0.15, 0.16	0.18, 0.20	0.10, 0.16	0.25, 0.08
CV	3.3, 1.7	3.8, 5.5	4.0, 5.6	2.1, 2.9	4.8, 2.4
	P^3 (L, W)	P^4 (L, W)	M^1 (L, W)	M^2 (L, W)	M^3 (L, W)
High	3.1, 3.7	3.9, 5.1	4.4, 5.2	5.0, 6.7	4.0, 5.2
Low	— —	— —	4.1, 5.0	4.5, 5.5	3.5, 4.8
n	1	1	3	6	7
Mean	— —	— —	4.2, 5.1	4.7, 6.2	3.8, 5.1
SD	— —	— —	0.12, 0.09	0.16, 0.40	0.15, 0.13
CV	— —	— —	2.9, 1.8	3.4, 6.5	3.9, 2.5

vicinity of the type section northeast of the town of Lost Cabin, and are both geographically and geologically restricted. Certainly the fauna from the Lysite Member alone cannot be said to represent all time elapsed between the Graybullian and the Lostcabinian. No taxon of *Hyopsodus* is restricted to the Lysite Member, although an abundance of *H. powellianus–powellianus* marks Lysitean strata in the Wind River and Bighorn basins.

The type of "*Hyopsodus browni*" (ACM 3232) is a smaller specimen of the *Hyopsodus powellianus* lineage rather than being referable to *H.* sp., cf. *H. mentalis,* based on its posteriorly extended hypocone on M^3, long anteroposterior length of P^3, and the degree of development of the hypocristid on P_4. Other specimens, such as CM 19834, are similar to ACM 3232 in size and also conform more closely to the diagnosis of *H. powellianus–powellianus.* If the Lysite Member sample, referred here to *H. powellianus,* does represent a mixture of *H. powellianus–powellianus* and *H.* sp., cf. *H. mentalis* (Kelley and Wood, 1954, and Guthrie, 1967, also support the presence of only one large Lysitean lineage of *Hyopsodus*), then there is considerable overlap between them in size and virtually complete overlap in morphology. Considering the morphology of *Hyopsodus* sp., cf. *mentalis* as it appears in the San Juan Basin and at the non-Lysite Member localities in the Wind River Basin, this appears to be an unlikely possibility. No specimens of undoubted *H.* sp., cf. *H. mentalis* morphology were identified in the CM or ACM collections from the Lysite Member. Larger specimens of *Hyopsodus* from the ?early Lysitean Cole localities (CM localities 1903 and 1904), approximately 60 km to the southeast (see Fig. 23, Table 2) in the Casper Arch area, correspond to the diagnosis of *Hyopsodus* sp., cf. *H. mentalis* and are referred to this taxon here.

Specimens from the ?Lysitean/?Lostcabinian Okie Trail and Pavillion localities (see larger specimens on histograms in Fig. 22) are nearly identical to *H.* sp., cf. *H. mentalis* as it is known in the San Juan Basin—significantly smaller and different in P_4 morphology than Lysitean specimens of *Hyopsodus powellianus–powellianus.* The referred lower dentitions are especially like *H.* sp., cf. *H. mentalis* in featuring a very large entoconid on P_4 and in lacking the more inflated talonid cusps typical of *Hyopsodus powellianus.* The size and morphology of this material are outside the range of any lineage segments of *Hyopsodus paulus,* and

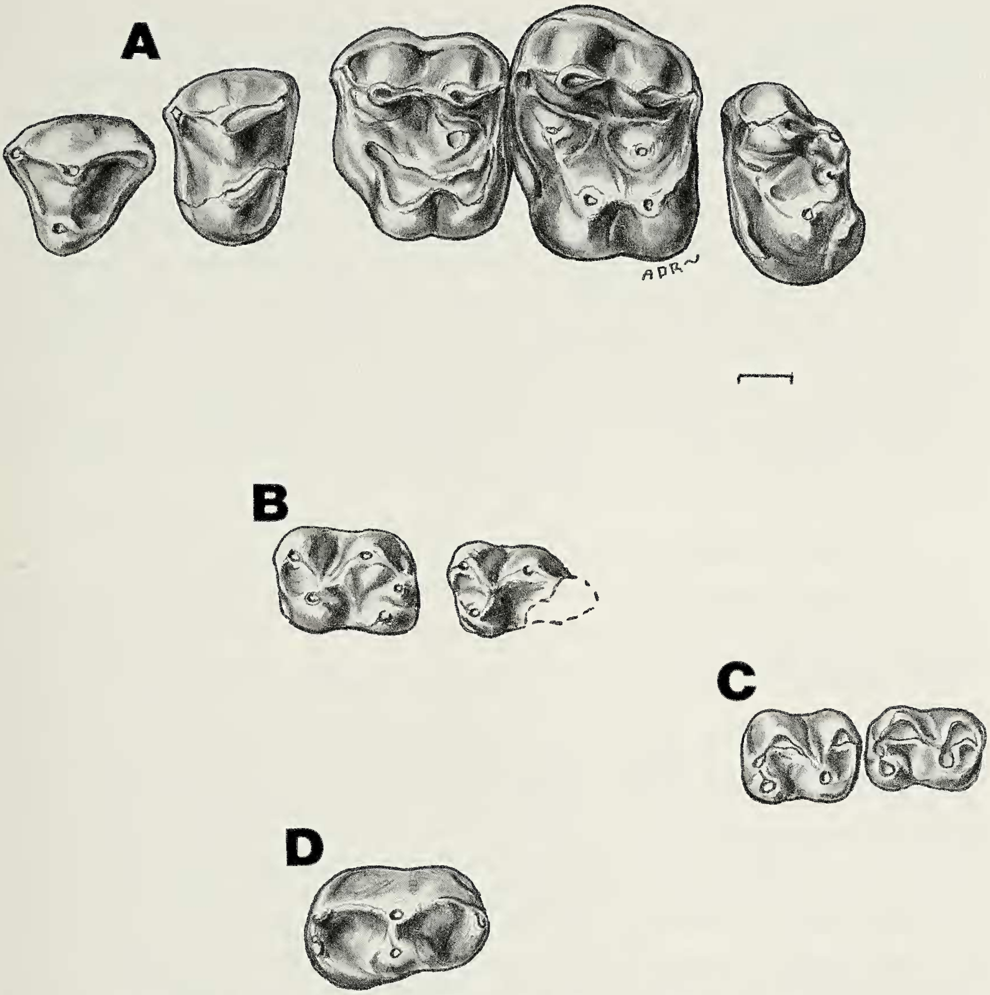

Fig. 23.—Specimens of *Hyopsodus* from localities other than the Lysite and Lost Cabin members of the Wind River Formation. A, CM 4915 (early *H. powellianus*) from the Piceance Basin; B, CM 10472 (*H. minor*) from the Piceance Basin; C, CM 445976 (?*H. minor*) from the San Juan Basin; D, CM 45996 (*H.* sp., cf. *H. mentalis*) from the ?early Lysitean Cole locality. Scale equals 1 mm.

similar *Hyopsodus* does not occur at any of the much better sampled, undoubted Lostcabinian localities in the Wind River Basin. The sample size from the Okie Trail and Pavillion localities is small (a total of 26 catalogued specimens) but this material may indicate a limited immigration from another source area, followed by a local extinction. At this point, this conclusion should be regarded as purely speculative. The biostratigraphic record of *Hyopsodus* sp., cf. *H. mentalis* or specimens similar to it terminates with these localities. It may be noted that Gingerich (1976*a*) reports two specimens from early Lostcabinian sediments of the Willwood Formation whose lower first molars cluster around a mean $\log_{10}$ of 1.25. They are attributed to a new *Hyopsodus* lineage trend but appear to be anomalous on the graph presented. *Hyopsodus* sp., cf. *H. mentalis* possesses molars that exactly correspond to Gingerich's anomalous specimens. The immigration of a distinct taxon is a better explanation for these and similar *Hyopsodus.*

Alternatively, the lower molar size distribution of *Hyopsodus* at the Wind River Okie Trail area could be interpreted as representative of an earliest Bridgerian time—representing a mix of *Hyopsodus paulus–paulus* and *Hyopsodus minusculus* (see discussion of small specimens under *H. minor*). For the present time, however, the P_4 morphology of specimens that preserve this tooth seems consistently derived with respect to the *Hyopsodus paulus* lineage and much more like that of San Juan Basin *Hyopsodus* of similar size. Five uncatalogued specimens containing P_4 collected since 1989 are virtually identical. Also, the representation of the large (intermediate) and small forms of *Hyopsodus* at Okie Trail is numerically biased in favor of specimens referred here to *H.* sp., cf. *H. mentalis*—different from Gardnerbuttean localities where *H. paulus* and *H. minusculus* occur with approximately equal frequency. Stratigraphic relations (Stucky et al., 1990) and the presence of *Lambdotherium* also suggest that the Okie Trail localities are early Lostcabinian rather than Gardnerbuttean.

KEY TO IDENTIFYING THE TAXA OF EARLY EOCENE *HYOPSODUS*

The following summary of change in *Hyopsodus* species-lineage taxa may be useful in discriminating *Hyopsodus* specimens from the Wasatchian and Bridgerian of North America.

Hyopsodus paulus is intermediate in size (see Tables 3, 4) and is detectably larger than *H. loomisi* at localities with a good sample size. In Graybullian *Hyopsodus paulus,* the lower third molars are short, generally equal to or shorter than the second molars. Lower premolars are long, but transversely wide (rather oval in occlusal view), bunodont with the trigonid cusps dominating the teeth. The paraconid is frequently large on the low-crowned lower molars. Upper molar hypocones and external cingula are not well formed but are stronger than those of *H. loomisi.* Lysitean *Hyopsodus paulus* retains relatively long lower fourth premolars, but has more defined protoconids and metaconids and more basined and proportionately longer talonids. M_3 is equal to or longer than M_2. Lower molar paraconids occur less frequently and are smaller; hypocristid and metacristid are stronger. Upper molars have distinct labial cingula and may show external ribs on exterior margins of the paracone and metacone. By the earliest Bridgerian, *Hyopsodus paulus* is somewhat larger in molar size and more derived on average in the degree of expression of characters mentioned above as well as shortening of the lower premolar series, anterior shifting of the molar protoconid and apex of hypoconid, lingual placement of the hypoconulid, labiolingual compression of upper molar and premolar paracone and metacone, and increased lophodonty of all cusps and the connecting crests between them. West (1979*a*) cites more strongly connected upper molar protocones and hypocones in Bridgerian *H. paulus,* however, analysis of the entire *H. paulus* lineage sequence suggests that this is an artifact of the development of wear facets, and can also be observed in Graybullian specimens. *Hyopsodus loomisi* more frequently shows a distinct valley between these cusps. *Hyopsodus paulus* is easily distinguished from significantly smaller lithosympatric *H. minor* and *H. minusculus.*

Hyopsodus powellianus enlarges in size through time and increases swelling of the cusps, prominence of the molar entostylid and P_4 posthypocristid, broadening of the upper premolar and molar anterior cingula as well as the hypocrista of M^3.

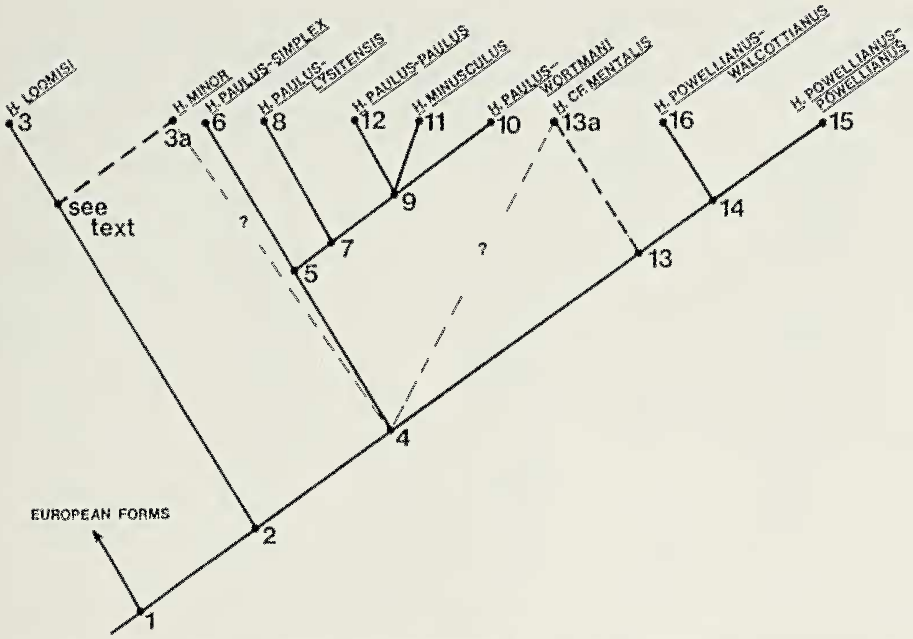

Fig. 24.—Proposed cladistic relationships of Wasatchian and early Bridgerian *Hyopsodus*. Characters discussed in text.

The compression of cusps noted in *Hyopsodus paulus* is not apparent in this lineage but, in parallel, it does show increase in relative size of upper and lower third molars, reduction of molar paraconids (usually to an even greater degree than lithosympatric specimens of *H. paulus*), and in the slight development of labial ribs on the upper dentition. Of course, as *H. powellianus* is the largest-sized taxon of *Hyopsodus*, it is easily discriminated at localities with a fair sample of *Hyopsodus*.

At the level of resolution undertaken in this revision, the phylogenetic pattern of *Hyopsodus* is one of gradually evolving morphologic lineages. One intermediate-sized lineage (*Hyopsodus paulus*) occurs throughout the Wasatchian and Bridgerian, and three smaller forms are related to this lineage at different evolutionary stages (*Hyopsodus loomisi, Hyopsodus minor,* and *Hyopsodus minusculus*), as are the large taxa *Hyopsodus powellianus* and *Hyopsodus* sp., cf. *H. mentalis.*

RELATIONSHIPS

If the diagnoses of all of the taxa of *Hyopsodus* are considered to be descriptions of discrete, nonchanging entities, then it is possible to construct a cladogram of the known Wasatchian and early Bridgerian taxa. Problems may arise because the dental characters are "average" morphologies and, in the case of lineage segments, parts of continua. Figure 24 is an illustration of the proposed cladistic relationships. Some nodes partly reflect more frequently expressed or more highly developed characters as opposed to a character's absolute presence or absence. The cladogram was constructed in order to discuss derived features at the numbered nodes as traits of morphologic discrimination. However, as mentioned ear-

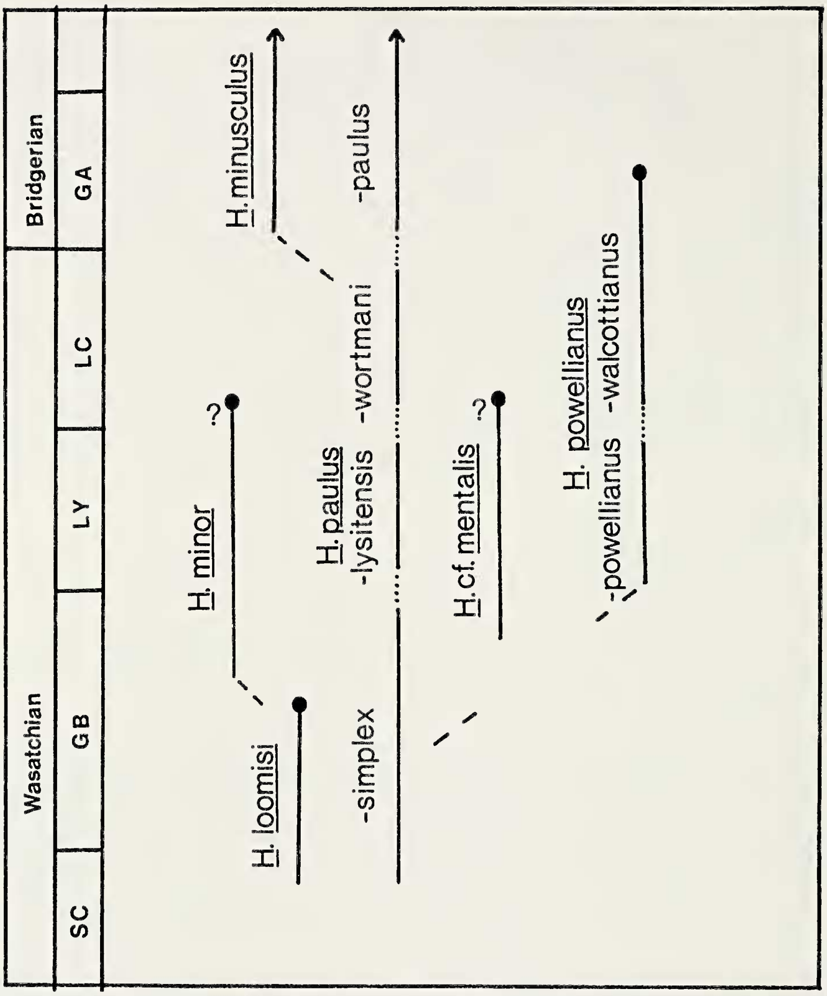

Fig. 25.—Proposed phylogenetic relationships of species and species lineages of Wasatchian and early Bridgerian *Hyopsodus*. Abbreviations; SC, Sandcouleean; GB, Graybullian; LY, Lysitean; LC, Lostcabinian; GA, Gardnerbuttean.

lier, this cladogram obscures evolutionary information inferred from the combination of a large number of specimens and sufficiently precise stratigraphic data. Therefore, a nondichotomous phylogenetic classification is also given (Fig. 25) The lineage-segment etymology used in this study expresses evolutionary and relationship statements in its informal trinomials as well. Due solely to cladistic convention, Figure 24 is a more complicated explanation of *evolutionary pattern* in *Hyopsodus* than is necessary.

Computer algorithms were not used to generate this tree. Many dilemmas were faced during the course of systematic work with *Hyopsodus*. The rooting of this tree was not a problem; *Hyopsodus* as a genus was not assessed for relationship to other generic-level taxa; therefore, what was considered primitive for a *Hyopsodus* taxon was based on relative time of occurrence of the character or its frequency. The variability of characters made them impossible to score either as present or absent or objectively on a "one-to-three" (for example) range. The initial weighing of character frequencies based on stratigraphic information would consequently weigh the ensuing cladogram.

Cladogram Node 1 describes the derived dental features of *Hyopsodus*. Arctocyonid condylarths and *Haplomylus* were used as outgroups. Derived features are: two primary cones on P^4; hypocone large and approaching height of protocone on M^{1-2} (much larger than any "pericone" on anterior cingula); distinct hypocone or hypocrista on M^3; lower molar hypoconulids enlarged and comparatively posterolingually oriented; M_3 hypoconulid relatively large, crescentic, and separated from hypoconid and entoconid; P_4 simple in cusp morphology, no ectoflexid or anteriorly placed paraconid; paraconid not structurally distinct on M_1 (if present, it appears as a cuspule on the preprotocristid). Some characters, such as P_{3-4} morphology and small, unspecialized anterior dentitions appear to be decidedly primitive for Eutheria as a whole. However, the retention and modifications of this morphology in *Hyopsodus,* as compared to many arctocyonids, meniscotheriids, phenacodontids, and other known faunal contemporaries, are unique among Eocene mammals of comparable or larger body size. The European forms of *Hyopsodus,* which are still incompletely known, seem to share the above described characters. Since they appear to be quite primitive they are portrayed in Figure 24, but were not cladistically resolved in this study. Very primitive fossils from the People's Republic of China will be described soon (M. R. Dawson and K. C. Beard, personal communication), but were also not included.

Node 2 lists the shared/derived characters of *Hyopsodus loomisi* and all other *Hyopsodus* from the North American early to middle Graybullian record. These are: very small upper and lower third molars; only partly distinct hypoconulid on M_3; low crowned, conical cusps on all teeth; very high frequency of vestigial paraconid on M_1, high frequency on M_2 and M_3; molar cingula relatively weak; P_{3-4} long and wide with large-based, amorphous protoconid (not distinctly differentiated from other trigonid cusps).

Unique characters of *Hyopsodus loomisi* (Node 3) are: small size; very low-crowned dentitions with poorly developed connecting lophs between cusps; transverse width of M^1 frequently close to width of P^4; anterior and external cingula severely reduced or absent on upper dentition; M^3 hypocone very restricted or absent, hypocrista weak, metacone not distinct; M^{1-2} hypocone small, somewhat labially situated and distant from protocone; lower molar entoconid small and labial; M_{1-2} trigonid width usually greater than talonid width.

Node 4 indicates shared/derived characters of all other forms of *Hyopsodus,* spanning the Graybullian to the Gardnerbuttean, exclusive of *Hyopsodus minor* (dental characters indicated by Node 3a below). These are: P^4 most frequently narrower than M^1; M^3 hypocone and metacone more highly developed, M^3 appears "somewhat bent" on posterior margin; more strongly developed protoloph on M^{1-3}, anterior and external cingula well defined; M^{1-2} hypocone strong, relatively lingual, and more nearly equal in height and size to protocone; P_4 paraconid more distinct; M_{1-2} with stronger and more lingually placed entoconid, transverse width of talonid usually greater than width of trigonid.

All members of the *Hyopsodus paulus* lineage are united by the shared or secondarily modified characters at Node 5. The most important and relatively static character here is intermediate size. Other characters dissimilar from the *Hyopsodus powellianus* lineage (Nodes 13–16, below) are: distinct but not expanded anterior cingula on the upper dentition posterior to P^2; M^3 metacone more labial, hypocone usually present but not part of posterior hypocrista flange; entostylid of lower molars, when present, is small and not inflated at base; molar metaconid less tall, protoconid not as anteriorly placed.

The Lysitean species *Hyopsodus minor* is represented at Node 3a. Some characters indicate it is most closely allied to *H. loomisi*; however, if this is a direct ancestor–descendant relationship, the "*H. loomisi–H. minor* lineage" also appears to have paralleled *H. paulus* in some aspects of anagenetic change. Although *Hyopsodus minor* shares small size, transversely compressed lower molar talonids, and weak hypocones on M^{1-2} with *Hyopsodus loomisi,* it also features proportionately larger upper and lower third molars, moderately developed cingula, shorter fourth lower premolars with an entoconid, and somewhat larger M^1. These features are, in turn, shared with Graybullian and Lysitean segments of the *Hyopsodus paulus* lineage. Unfortunately, the upper dentition of *H. minor* is not well known in the Wind River collections, and its diagnosis is based on limited material. A greater number of *Hyopsodus loomisi* upper dentitions were examined in this study. Upper molars of *Hyopsodus minor* appear more transversely compressed or "fat" than most other *Hyopsodus,* but not as square in occlusal view or with as continuous cingula as *Hyopsodus minusculus.* Some specimens have weak ribs on the external margins of the paracone and metacone as in *H. paulus.*

Node 6 defines the morphology of lineage segment *Hyopsodus paulus–simplex,* if this taxon is treated as a static entity, rather than an informal, most primitive stage of *Hyopsodus paulus.* Characters at this node are the same as those listed at Node 5, expressed to the degree indicated by the lineage-segment diagnosis in practically all specimens.

Node 7 represents the informal boundary point of frequently expressed derived features separating specimens of *Hyopsodus paulus–lysitensis* from the temporally preceding *H. paulus–simplex.* As with the Nodes 5 and 6 combination, Node 8 merely marks the presence of the character states of Node 7 in the vast majority of specimens. Node 7 indicates: slight transverse compression of upper premolar paracone and upper molar paracone and metacone; M^3 nearly as labiolingually wide as M^1; external ribs expressed more frequently; entoconid more nearly separate from hypoconulid on all molars, particularly M_3; P_4 shorter, protoconid more distinctly separate from other trigonid cusps, entoconid common on posthypocristid; P_{3-4} with relatively longer talonids (as compared to general trigonid length); lower molar paraconid and entostylid less common.

At Node 9 are the more advanced characters shared by the Lostcabinian and Gardnerbuttean small and intermediate lineages of *Hyopsodus.* These are: transversely compressed paracones and metacones on upper cheek teeth with strong labial ribs; M^3 metacone well developed and labially situated; anterolabial wings of protocone on P^{3-4} and loph between upper molar protocone and paraconule stronger; shorter lower premolar series; infrequent occurrence of paracone on M_1, very infrequent paracone on M_2; hypoconulid lobe of M_3 well developed and more nearly separate from entoconid and hypoconid on majority of specimens; generally more lophodont (crests more distinct, cusps less so) dentition. These characters also describe *H. paulus–wortmani* (Node 10), which is morphologically "intermediate" between and temporally precedes both of the Bridgerian forms, *H. paulus–paulus* and *H. minusculus.* No autapomorphies distinguish *H. paulus–wortmani.* Node 9 is at a trichotomy rather than as a sister group to *H. minusculus* or *H. paulus–paulus* because it is impossible to determine which of the latter taxa share more in common with *H. paulus–wortmani.*

Hyopsodus paulus–paulus and *H. minusculus* (Nodes 12 and 11) share the characters of *H. paulus–wortmani* (Nodes 9 and 10) in common, but differ in the following ways. *Hyopsodus minusculus* (Node 11) is derived in the high frequency of occurrence of: small size; shortened P_4 with anteriorly inflected paraconid and elevated labial margins of hypocristid with no entoconid (tooth appears notched); more elongate lower molars with hypoconulid often separated from entoconid by a notch; molar cristid obliqua meets trigonid somewhat more labially; upper molars not as wide (more nearly square than) as in *H. paulus–paulus,* paraconule small and not crescentic; hypocingula of M^3 not as posteriorly expanded, more closely follows posterolingual base of protocone.

Hyopsodus paulus–paulus (Node 12) is distinguished by: uniformly larger than *H. minusculus* (average size also larger than *H. paulus–wortmani*); lingual shifting of M_1 and M_2 hypoconulid; entoconid more anterolingually distant from hypoconulid and often connected by strong crest; more anteriorly placed molar protoconids and generally more lophodont crests; P_4 shorter than in *H. paulus–wortmani*; P_4 more distinctly basined (not severely notched) with entoconid more common than in *H. minusculus*; P_4 metaconid more distinct; wider upper molars (especially M^2) than in *H. minusculus,* more distinct and crescentic paraconules; more extensive hypocrista on M^3.

Node 13 describes the derived characters of large Wasatchian and early Bridgerian *Hyopsodus.* These are: large size, anteriorly expanded cingula on upper dentition, larger parastyle on P^{3-4}, M^3 metacone strong but somewhat more lingual in comparison to paracone, long P_4 with well-defined talonid, relatively large M_{1-2} hypoconulid. This diagnosis also defines specimens of *Hyopsodus* sp., cf. *H. mentalis* (Node 13a), which is close to the *Hyopsodus paulus* lineage at the Lysitean stage but is significantly larger and usually features a very strong entoconid on the posterolingual margin of the P_4 posthypocristid. In the latter character, *H.* sp., cf. *H. mentalis* is most similar to lineage segment *H. paulus–simplex* or *H. paulus–lysitensis,* whereas molar size is closer to the *Hyopsodus powellianus* lineage.

Node 14 represents shared/derived characters of the *Hyopsodus powellianus* lineage. At this node are: very large size, P^3 triangular in occlusal view, bases of protocone and hypocone on M^{1-2} swollen, hypocrista and hypocone of M^3 posteriorly splayed (amplification of "bent" character discussed at Node 4), lower molar entostylid and metastylid very common and large, posthypocristid on P_{3-4} strong (entoconid variably present on P_4) and often partially encloses talonid, hypoconulid lobe of M_3 very large.

The differences between lineage segments *H. powellianus–powellianus* and *H. powellianus–walcottianus* are shown above Node 14. Node 15, the character states of *H. powellianus–powellianus,* indicates: lower molar metaconid large and tall, paraconid absent or very reduced on M_{2-3} (less frequently present or as large as in the *Hyopsodus paulus* lineage); entostylid and entoconid variably large and aligned with hypoconulid on lower molars. Otherwise, all *H. powellianus–powellianus* specimens conform to the diagnostic characters of Node 14, at least those from the Lysitean of the Wind River and Bighorn basins.

Hyopsodus powellianus–walcottianus (Node 16) is distinct in its extremely large size; very large entostylids on lower molars; molar protoconids anteriorly oriented; very rectangular P_4 with strongest posthypocristid of all *Hyopsodus*; and possibly, larger hypocone on hypocrista of M^3.

As has already been discussed, some of the best defined "monophyletic" taxa represented in this cladogram are the relatively poorly known ones—those with either a limited record or those from single temporal intervals. For example, specimens of *Hyopsodus minor* are underrepresented in the Eocene record except in the Lysite Member of the Wind River Formation, where they appear quite distinct from other lithosympatric *Hyopsodus*. The same is true of *Hyopsodus powellianus–walcottianus*. Both taxa, distinct at single biostratigraphic levels, show overlap with specimens from preceding intervals—the former with Piceance Basin *H. minor*, the latter with specimens of *H. powellianus–powellianus*. Given the evidence for considerable anagenesis between successive specimens of *H. paulus*, it is apparent that what are designated here as taxonomically "stable" forms do change through time and that expressing this change in a cladogram may distort what can be inferred of paleobiologic reality.

The "species" *Hyopsodus paulus* is paraphyletic; *Hyopsodus powellianus* would be also, if *H. powellianus–powellianus* is the sister taxon of *H.* sp., cf. *mentalis*. The cladogram depicts *Hyopsodus paulus–paulus* as the sister taxon of *H. minusculus*, with each preceding lineage segment of *Hyopsodus paulus* being successively more primitive. *Hyopsodus paulus–lysitensis* and *H. paulus–simplex* are united with *Hyopsodus paulus–paulus* only on the basis of primitive characters. If the species is the operational unit of a cladogram, then the lineage-segment taxa are noncladistic. This is an example of how species-lineage segments are difficult to resolve cladistically because, by definition, they have arbitrary boundaries based on the combination of frequency of character expression and overlain stratigraphic data. The species *Hyopsodus paulus* is paraphyletic. Paraphyly is, without question, a cladistic sin, but does not trespass on the description of biologic change through time. Lineage segments go further; they attempt to describe change over time. Recognizing these conflicts, it is worthwhile to review and summarize the overall pattern of *Hyopsodus* evolution (Fig. 25). The conclusions of this study reflect the choice of simplifying *Hyopsodus* taxonomy by allying specimens of similar, but not exactly the same, morphology over the option of resurrecting the numerous geographic and temporal species of past workers. This reflects a philosophy regarding paleontological "species" and an attempt to discern a pattern of morphologic change and overlap as taxa proceed through time.

One fact concerning the diversity of Wasatchian and early Bridgerian *Hyopsodus* is true for all localities. **Never** are more than three species of *Hyopsodus* found in lithosympatric association. Generally, these taxa can be classified as small, intermediate, and large in size. Two fundamental considerations argue against concluding that this is an indication of evolutionary stasis within early Eocene *Hyopsodus* taxa. First, each species lineage (lineage, not segment), defined on derived features at the point of its first observable dental distinction, undergoes considerable anagenetic change through time. For example, *Hyopsodus paulus–paulus* is very distinct from *H. paulus–simplex*. *Hyopsodus paulus–simplex* as a discrete taxon (ignoring subsequent lineage segments of *H. paulus*) is morphologically much closer to *Hyopsodus loomisi* owing to the more frequent occurrence of primitive characters such as small third molars and molar paraconids. Were it not for other key character differences that are later canalized and far more strongly expressed (anagenesis), *H. paulus–simplex* and *H. loomisi* could not be as readily distinguished. *Hyopsodus paulus–paulus* represents a form which

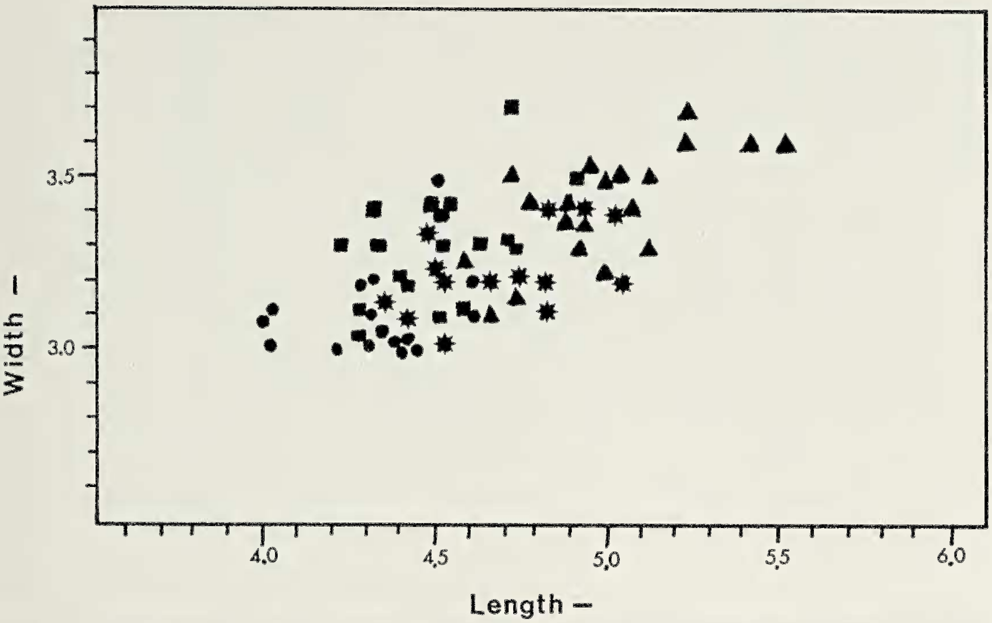

Fig. 26.—Length/width plot of *Hyopsodus paulus* lower third molars from selected localities. Horizontal and vertical axis are in mm. Symbols: circles, Graybullian, Dorsey Creek; squares, Lysitean, Davis Draw; starbursts, Lostcabinian, "K-6, B-2 horizon"; triangles, Gardnerbuttean, CM loc. 34 (20 randomly selected specimens).

more strongly and more frequently emphasizes characters first appearing in *H. paulus–simplex,* such as large molar hypocones, well-distinguished cingula, and wide lower molar talonids. Anagenetic increase in the comparative size of the lower third molar of *Hyopsodus paulus* is portrayed in Figure 26. The relative size of M^3 parallels this development. Like the *Hyopsodus paulus* lineage, *Hyopsodus powellianus–walcottianus* is larger and emphasizes derived dental morphology found in its Lysitean ancestors.

Another argument against stasis in early Eocene *Hyopsodus* is the evidence that taxa of similar size (*H. minor, H. minusculus*) evolved iteratively in the Wasatchian and early Bridgerian. This pattern was strongly indicated by Gingerich (1974*a*), based on the change in size of M_1 through time in the Bighorn Basin (Fig. 27), and is more generally corroborated by dental characters in this study. What this evolutionary pattern implies remains uncertain; Gingerich (1974*a*) failed to remark on the systematic implications or geographic extrapolation of *Hyopsodus* evolution outside of a single basin. As yet, the role of immigration of closely related forms has still not been discussed. Resolving these problems (with any fossil taxon) remains a problem for future paleontological research. Less formal examination of *Hyopsodus* from Bridgerian and Uintan localities suggests that West's (1979*a,* 1979*b*) declaration of stasis as the rule for later Eocene lineages can no longer be accepted or cited as valid. Only size is relatively constant in the Bridgerian. Preliminary, unpublished research does indicates morphologic change during this interval.

The small forms *Hyopsodus minor* and *Hyopsodus minusculus* are not closely related (based on a lack of shared/derived attributes other than size) and are

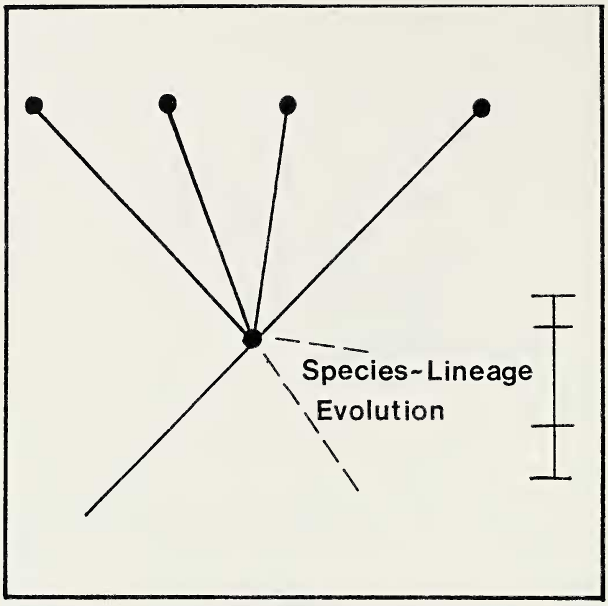

Fig. 27.—Pattern of *Hyopsodus* evolution in the Willwood Formation, as determined from $\log_{10}$ of length × width of first lower molar. From Gingerich, 1974*a*.

temporally disjunct. Wind River *H. minor* appears to be close to *Hyopsodus loomisi* in certain key characters (see above) and is very similar to the slightly larger specimens from the San Juan and Piceance basins. *Hyopsodus minusculus,* on the other hand, possesses many advanced characters in common with *Hyopsodus paulus–paulus* and, other than being smaller in average size, closely corresponds in morphology to some specimens of Lostcabinian *Hyopsodus paulus–wortmani.* Therefore, it seems that two small lineages of *Hyopsodus* evolved independently during the early Eocene and that the synonymy of *Hyopsodus minor* and *H. minusculus* (= "*H. wortmani*" of previous studies; Gazin, 1968) is not correct. At least within the Wind River Basin, this appears to be an example of iterative evolution of similar size types within the same genus. As another example, in the late Eocene, *Hyopsodus uintensis* (Osborn, 1902) and *Hyopsodus sholemi* (Krishtalka, 1979) became almost as large as Wasatchian *Hyopsodus powellianus,* but there is no evidence the former are related to the latter. Large-sized *Hyopsodus* is completely absent from the intervening and densely sampled Bridgerian localities of the Rocky Mountain Interior (Gazin, 1968; West 1979*a,* 1979*b*). In the early to middle Wasatchian, *Hyopsodus* sp., cf. *H. mentalis,* possibly the result of an iterative southern radiation, may also have occupied a large *Hyopsodus* niche, particularly in the basins south of Wyoming.

Hyopsodus paulus is abundantly known from earliest through latest Wasatchian localities; although it undergoes directional change in dental morphology, it shows little increase in molar size in this interval. Members of this lineage are probably ancestral to *Hyopsodus powellianus, Hyopsodus minusculus,* and possibly *H.* sp., cf. *H. mentalis* at different times in its Wasatchian history. Relationship with *Hyopsodus powellianus* is supported by shared/derived characters, whereas the gradual divergence of *H. minusculus* can be more directly inferred from lithologically successive populations of *Hyopsodus* from the late Lostcabinian and Gardnerbuttean of the Wind River Formation. A similar gradual divergence has been noted in *Leptomeryx* from the Chadronian Flagstaff Rim area of Wyoming (Heaton, 1989), although in this study of *Hyopsodus,* no judgments are made concerning sympatric speciation. Again, although *Hyopsodus paulus* may indeed comprise many closely related biological species and subspecies, as a group, all the specimens share morphology not expressed with a similar frequency in other *Hyopsodus* taxa. The reasons *Hyopsodus paulus* is recognized as a single species lineage for specimens from the earliest to middle Eocene (see Table 1, the type is Blacksforkian) are twofold: (1) an intermediate-sized lineage of *Hyopsodus* (i.e., *H. paulus*) can be differentiated comparatively at practically all localities within this long interval. The examination of intermediate-sized specimens suggests a morphologic continuum (anagenetic rather than cladogenetic) when arranged in bio- or lithostratigraphic order. Although possible speciation events in this lineage cannot be abstractly rejected as possibilities, there is no positive evidence to support them; and (2) naming geographic or stratigraphic species would expand the species diversity of the genus without any proof of cladogenesis (see Krishtalka and Stucky, 1985). Subspecies seem inappropriate for the fossil record given that workers rarely agree on species definitions and because they were never meant to denote temporally successive taxa.

Specimens of *Hyopsodus paulus* from the Lostcabinian (*H. paulus–wortmani*) may represent two biological species (one being incipient *H. minusculus*) from this time period, at least in the Wind River Basin. However, the overlap of characters and the normal size distribution from single localities cannot be systematically unravelled. These characters are associated with intermediate and small-sized populations of *Hyopsodus* (*H. paulus–paulus* and *H. minusculus*) in the earliest Bridgerian. This "mixed" assessment of *H. paulus–wortmani* dental morphology could not have been identified without knowledge of the morphological distribution of temporally succeeding Bridgerian specimens of *H. paulus–paulus* and *H. minusculus.*

Apparently, *Hyopsodus minusculus* continued to average smaller in molar size throughout the Blacksforkian. *Hyopsodus minusculus* M_2 length averages 3.28 mm at Church Buttes (low Bridger B, USNM collections) according to West (1979*a*: 32), smaller than at CM loc. 34 (Gardnerbuttean), and similar in size to Lysitean *H. minor.*

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE

The abundance of *Hyopsodus* has been cited as a drawback for complete systematic review. Systematics aside, data concerning the frequency of occurrence of taxa of *Hyopsodus* at localities may bear on interpretations of their paleoecology and distribution. These matters are considered in this section.

The total number of *Hyopsodus* specimens collected from the Wind River Basin, tallied from the CM specimen catalogue, are listed in Table 11. These numbers are approximate and may be low estimates, particularly for *Hyopsodus powellianus–powellianus, Hyopsodus paulus–paulus, Hyopsodus paulus–lysitensis,* and *Hyopsodus minusculus,* because many older CM catalogue numbers may refer to batches of five to 50 isolated jaws and teeth, some of which can be fragmentary or represent two or more taxa. The totals are qualitatively (proportionately) fairly accurate even though the absolute number of specimens is much higher.

Table 11.—Approximate number of CM specimens of *Hyopsodus* taxa tallied by catalogue number counts. Specimens counted are from the Lost Cabin and Lysite members of the Wind River Formation.

Taxa	Approximate number of CM specimens
Gardnerbuttean	
H. paulus–paulus	320
H. minusculus	260
H. powellianus–walcottianus	1
Lostcabinian	
H. paulus–wortmani	160
H. powellianus–walcottianus	11
Lysitean	
H. paulus–lysitensis	310
H. powellianus–powellianus	440
H. minor	35

In the Gardnerbuttean of the Wind River Formation, the intermediate-sized *Hyopsodus paulus–paulus* and the small *Hyopsodus minusculus* occur in relatively equal numbers, comprising 55 and 45 percent of total specimens, respectively. Twenty field seasons of prospecting in the Gardnerbuttean have only recently yielded one specimen of *H. powellianus–walcottianus,* from less intensively examined upper grey beds at CM loc. 34. Stratigraphically lower, in the Lostcabinian of the Lost Cabin Member, *Hyopsodus paulus–wortmani* outnumbers the much larger *H. powellianus–walcottianus* 94 percent to six percent. More recent collecting has added about 100 catalogued and uncatalogued dentitions of *H. paulus–wortmani.*

The *Hyopsodus* size distribution in the Lysite Member of the Wind River Formation contrasts markedly with that of the Gardnerbuttean and Lostcabinian of the Lost Cabin Member. Here again, the intermediate-sized *Hyopsodus paulus* (*lysitensis*) is well represented by 40 percent of total specimens. However, the large form, *H. powellianus–powellianus* is even more common at 56 percent of total *Hyopsodus.* The small *H. minor* (four percent of total) is not common—and four percent may be a high estimate because many specimens of this species were separated from their original CM "batch" number and recatalogued under individual numbers during the course of this study to increase sample size.

The possibility that these differences in specimen abundance are due to collecting biases is fairly remote. Although the Lysite Member as a whole is generally somewhat more coarse-grained than the Lost Cabin Member, both the collecting procedures and the size of fossil elements found are the same. *Hyopsodus minor* specimens are no more difficult to find when surface prospecting than those of small primates, carnivores, and insectivores that are commonly recovered. *Hyopsodus minusculus,* similar in size to *H. minor,* is as frequently collected from Bridgerian localities as is the larger *H. paulus.* It does not appear likely that sorting or accumulation differences among mudstone horizons are responsible for the frequency of occurrence of *Hyopsodus* taxa in surface finds.

As a contrast to surface prospecting tallies, at the Lostcabinian CM Buck Spring Quarries, the relative abundance of *Hyopsodus* (see Stucky et al., 1990; data through 1988) is only five of 369 mammal specimens, versus 18 of 82 total specimens obtained by prospecting this area. The quarry sample is dominated by very small taxa and represents differential preservation (see Stucky et al., 1990) from the surrounding floodplain mudstones.

Outside of the Wind River Basin, the representation of *Hyopsodus minor* in the DeBeque Formation of Colorado is much better (Kihm, personal communication, 1989). Most well-preserved upper dentitions examined from the CM collections are from the Piceance Basin. If *Hyopsodus* as a whole is preferentially preserved because it was very common, as indicated by the data of Stucky et al. (1990), then probably, like *Meniscotherium* in the Lostcabinian (Gazin, 1965), *H. minor* was never common in the Wind River Basin. A similar phenomenon may explain the paucity of *Hyopsodus powellianus–walcottianus* specimens in the Lostcabinian. Gazin (1965) suggested that large *Hyopsodus* and *Meniscotherium* were incompatible, although neither taxon is common in the Lostcabinian of the Wind River. Other possibilities might be that taxa of *Hyopsodus* were environmentally specific or subject to broader competitive exclusion than that implied by competition with a single taxon (in this case, *Meniscotherium*).

Considering the factors discussed above, the following conclusions are offered as explanations for the pattern and frequency distribution of *Hyopsodus* in the Wind River Basin: (1) *Hyopsodus minor* was uncommon (less so than in the Bighorn and southern basins) and is restricted to the Lysite Member and CM localities 936 and 1903. It is possible that *H. minor* may have favored a paleoenvironment different from that of the Wind River Basin margins in the early Eocene, or, alternatively, was becoming rare by the time of Lysite Member deposition. This cannot be tested because aside from the Lysite Member, Lysitean time is very sparsely represented in the basin; (2) the large form, *H. powellianus–powellianus* is very common in sediments of the Lysite Member and may have been better adapted to this environment. This abundance of a large species may conflict with Gingerich's (1989) findings of smaller congeners in high-floodplain assemblages. Bown and Beard (1990) note the most frequent occurrence of large *Hyopsodus* intermediate to distal from paleochannel location as well. The Lysite Member may not fit a Bighorn Basin sedimentological model. The closely related but significantly larger *H. powellianus–walcottianus* persists from the Lostcabinian into the Gardnerbuttean in very reduced numbers, perhaps suffering in competition with other faunal elements of similar size; (3) the Gardnerbuttean horizons of the Lost Cabin Member are the first to preserve abundant numbers of small *Hyopsodus*—*H. minusculus*—which may have been well adapted to a mature river environment and associated forest canopy (as indicated by the abundance of arboreal faunal elements; see Stucky et al., 1990). The establishment of this environment in the Lostcabinian may have favored the evolution (or immigration) of *H. minusculus*. Even in the Lostcabinian, many specimens of *H. paulus–wortmani* are almost as small in tooth size as *H. minusculus*; and (4) intermediate-sized *Hyopsodus* are common at virtually all known early through middle Eocene localities in the Wind River Basin and western North America. It may have been the least habitat-restricted early Eocene *Hyopsodus*.

It is more difficult to comment with any confidence on the overall distribution of *Hyopsodus* taxa. The degree of interconnection of the western Eocene basins remains to be established. Debates on Laramide orogenic timing, degree of basin development, and classification are still in progress. Because mammalian biostratigraphy is the primary precise correlative tool for interbasinal sediments, taxa are used as indices of time. Biostratigraphy often suffers in that there is little consistency in the fossil species concept and because index taxa are often assumed

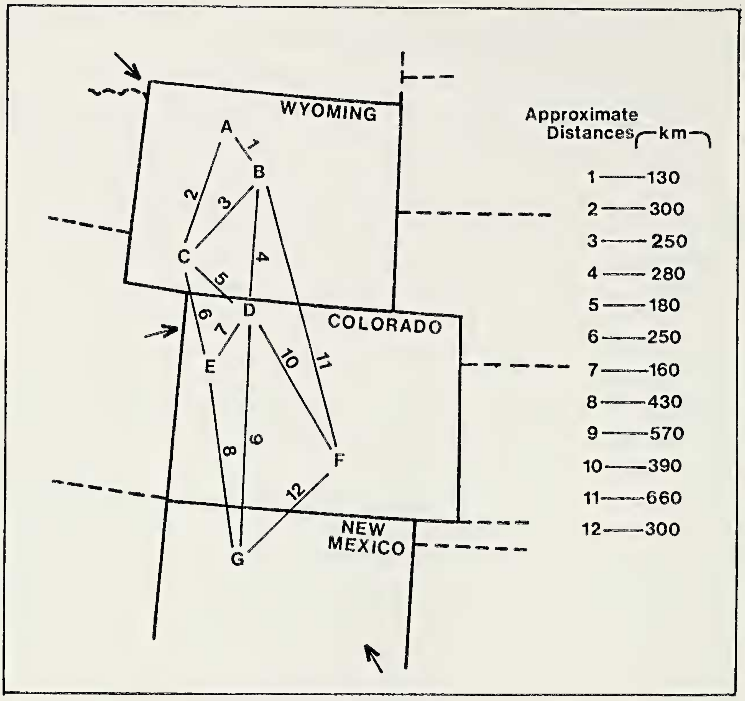

Fig. 28.—Relative distances between major western basins containing Wasatchian and early Bridgerian deposits. A, Bighorn Basin; B, Wind River Basin; C, Green River Basin complex; D, Four Mile area of "Wasatch Fm."; E, Piceance Basin; F, Huerfano Basin; G, San Juan Basin.

to be applicable as time indicators in all basins. If evolution is identified using the axis of time, and, conversely, time (biostratigraphy) needs the axis of evolution, then there is no independent data available to falsify hypotheses. If the immigration of an exotic taxon can be established, biostratigraphy is on firmer ground. However, because immigrations may depend on paleoenvironment and are not absolute time indicators, their resolution may be too coarse for anagenetic studies. These constraints can severely impact the study of vicariance and geographic distribution.

It may be possible to draw some preliminary conclusions based on the distances between Eocene basins. Absolute distances do not account for barriers or environmental differences, although their effects should not be discounted.

Of all the distances portrayed in Figure 28, that between the Bighorn and Wind River basins (Distance 1) is the least. Because the best record in each basin preserves mostly different biostratigraphic time, their respective faunas have long been strapped together to represent the Wasatchian Land Mammal Age. The characters and variation in size of *Hyopsodus powellianus* between these closest of basins in the Lysitean (based on biostratigraphy) suggest some ecological and faunal differences are present despite their relative geographic proximity. While this phenomenon may mimic modern differences between isolated basins, it may also indicate that the biostratigraphic correlation tying the Wind River and Bighorn basins is subject to the same effects. *Hyopsodus minor* may be another example of an environmentally specific taxon of *Hyopsodus*. It seems to be present in the Lysitean of the Bighorn (Buffalo) Basin to the north (Gazin, 1968), it is fairly common in the Piceance and San Juan basins to the south, and scarce in the intervening Wind River Basin. Unless the divergence of small *Hyopsodus* occurred in all basins at the same time, this would imply a northern origin and subsequent southern migration of *Hyopsodus minor* (refer to the distances to E and G).

If *H. minor* is a real biologic entity and not merely an alliance of unrelated taxa, then the simplest explanation for its range is that it was widespread in the Graybullian/Lysitean of the Rocky Mountain Interior and its emergence may have been an intrageneric response to homogeneous community conditions in some basins, partitioning space within *Hyopsodus* as a whole. Its poor record in the Wind River Basin is a reflection of the paleoenvironment of the Lysite Member.

Unfortunately, the record from southwestern Wyoming is not stratigraphically controlled (see the plethora of *Hyopsodus* species referrals in Gazin, 1962), and the record from the Huerfano and Piceance basins do not overlap sufficiently with the better known records from other basins. This makes it difficult to assess whether the same *Hyopsodus* species were truly common to all the Wasatchian basins. The similarity in the *Hyopsodus* record in the Wind River and Huerfano basins (Lostcabinian to Gardnerbuttean) supports the hypothesis. The distance between these basins (Distance 11) is large. Dispersal between the Huerfano and Wind River basins along the eastern Laramide front was proposed by Sullivan (1986) to explain the common occurrence of the anguid lizard *Eoglyptosaurus donohoei*; this route may have also accommodated small-bodied mammals.

The large species *Hyopsodus powellianus* also seems to have been extensive in its North American distribution, except for either faunal level of the San Jose Formation. At least in the Lysitean, *H. powellianus* was smaller south of the Bighorn Basin (such as in southwestern Wyoming and in the Wind River Basin). The largest lineage segment of *Hyopsodus powellianus* (the post-Lysitean *H. powellianus–walcottianus*) possibly had its origin to the north; Bighorn Basin Lysitean specimens approach lineage segment *walcottianus* in size. Some Wind River Lysitean specimens are close to *H. powellianus–walcottianus* as well. In the Piceance Basin, Kihm's (1984) "*H. powellianus* event" seems to have marked an immigration (crossing distances 2, 3, 4, and 6) of *H. powellianus,* a species that never reached or was never common in the San Juan Basin. Yet, this species was present in the later Wasatchian of the Huerfano Basin, still north, but not geographically far from the San Juan Basin (Distance 12). The inability of the New Mexican record to "fit" with the northern record suggests that the fauna and paleoenvironment of the San Juan Basin indeed was different.

Hyopsodus paulus, on the other hand, spans the entire Wasatchian and Bridgerian, and is known even from the San Juan Basin, which otherwise features an atypical *Hyopsodus* assemblage. *Hyopsodus paulus* shows enough consistent anagenetic evolution both within and between basins to justify the conclusion that it was present everywhere and possibly was a genetically continuous biological entity through the entire early Eocene of the Rocky Mountain Interior.

In the Wind River Basin, specimens of *Hyopsodus* from the Okie Trail and possibly the Pavillion Butte area are curiously similar to *Hyopsodus* from the Almagre of the San Juan Basin. The taxa of *Hyopsodus* from these areas are not satisfactorily resolved in this study, and more detailed knowledge on the relationship of faunas from these areas might shed new light on this anomaly.

So what may be said about the validity of *H.* sp., cf. *H. mentalis*? The diagnosis given in this study unites all specimens assigned to this taxon. Its occurrence in the Bighorn (as "*H. lemoinianus*"), Wind River (referred CM specimens), and San Juan basins suggests it was a wide-ranging form of Wasatchian *Hyopsodus.* However, aside from the San Juan Basin, it is certainly not common, an unusual condition for *Hyopsodus* taxa. If this taxon is not arbitrary, then the most reasonable, yet cautious, conclusion would be that many specimens of *H.* sp., cf. *H. mentalis* are representative of the *Hyopsodus paulus–Hyopsodus powellianus* divergence. However, this event must have occurred long before the Lostcabinian, presumably well before the time of deposition of Okie Trail and Pavillion Butte localities sediments. In the Wind River Basin, *Hyopsodus* sp., cf. *H. mentalis* does not occur with *H. powellianus* at the same locality. In the San Juan Basin, *Hyopsodus powellianus* is unknown. In the Piceance Basin, *Hyopsodus powellianus* may have replaced *H.* sp., cf. *H. mentalis* (Kihm, 1984). The "gradually separating" pattern of *Hyopsodus* evolution coupled with intra- and intergeneric competition is not at odds with the general implications of this conclusion. In the case of *H.* sp., cf. *H. mentalis,* better resolution may be hampered by too many geographic and stratigraphic gaps.

CONCLUSIONS

Two lineages of *Hyopsodus* existed during the Wasatchian and earliest Bridgerian of western North America. One of these lineages, *Hyopsodus paulus,* is common at all known localities and persisted after the Gardnerbuttean into the later Bridgerian. In order to describe more fully its pattern of change through time, *H. paulus* is divided into lineage segments. *Hyopsodus paulus–simplex,* the most primitive segment of *H. paulus,* is represented by specimens from the Sandcouleean and Graybullian. The anagenetically more progressive *H. paulus–lysitensis* segment denotes late Graybullian through Lysitean *Hyopsodus paulus.* Lostcabinian and Gardnerbuttean populations of *Hyopsodus paulus* are named *H. paulus–wortmani* and *H. paulus–paulus,* respectively.

The second lineage, *Hyopsodus powellianus,* is much larger in tooth size and probably diverged from *H. paulus* in the Graybullian. It is not known from the Graybullian localities examined in this revision, but is distinct by the Lysitean. *Hyopsodus powellianus* (lineage segment *powellianus*) is very common in the Lysitean of the Wind River and Bighorn basins and continues through the Lostcabinian (as lineage segment *walcottianus*) in reduced numbers. One specimen records its youngest occurrence in the Gardnerbuttean of the Wind River Formation.

In this study, the diagnosis of *Hyopsodus loomisi* is expanded to include characters of the lower dentition as well as expected morphological variation similar to that of other *Hyopsodus* taxa. *Hyopsodus loomisi* co-occurs with *H. paulus* in the Sandcouleean and a large portion of the Graybullian.

The small *Hyopsodus minor* was possibly present by the mid- to late Graybullian of the Bighorn Basin and is known from the Piceance and San Juan basins. It coexisted with *H. paulus* and *H. powellianus* in the Lysitean of the Wind River and Willwood formations.

A second small species of *Hyopsodus,* closely tied to *H. paulus–wortmani,* is first distinguishable by the earliest Bridgerian (Gardnerbuttean). This species, *Hyopsodus minusculus,* is as common as *H. paulus–paulus* at CM loc. 34 in the uppermost Wind River Formation. CM loc. 34 represents the only Wind River

Formation locality where very large numbers of a small and intermediate lineage of *Hyopsodus* co-occur.

Other specimens have been morphologically allied under *Hyopsodus* sp., cf. *H. mentalis,* although its biostratigraphic record and geographic distribution suggest it may be an unnatural grouping.

Detailed investigation of CM material from the Wind River Basin (over 3000 catalogue numbers, approximately 6000 total specimens) confirms the presence of four taxa (not including the uncommon and thus far presumed immigrant *H.* sp., cf. *H. mentalis*) of *Hyopsodus* in the early Lysitean through Gardnerbuttean—spanning what is now assumed to be between two to over three million years (Krishtalka et al., 1987). During this time interval, *H. minor* became extinct, *H. paulus* and *H. powellianus* evolved anagenetically, and one new taxon of *Hyopsodus, H. minusculus,* appeared. This does not appear to represent a rapid rate of cladogenesis within Wasatchian and early Bridgerian *Hyopsodus.* However, anagenesis affected the changing morphology of both *H. paulus* and *H. powellianus.* Anagenetic rate differed between the two lineages. For example, specimens of Lostcabinian *H. powellianus* are morphologically distinct from those of its putative Lysitean ancestor, whereas in the *H. paulus* lineage, Lostcabinian specimens are less so.

Given the relationships proposed here, the rate of cladogenesis is one taxon (in this case, *H. minusculus*) per two to 3.5 million years, or 0.29 to 0.50 (per million years). If "anagenetic taxa" are also considered new, then *H. powellianus–walcottianus* and *H. paulus–paulus* could be added to *H. minusculus.* The evolutionary rate would therefore increase to between 0.86 and 1.50. *Hyopsodus paulus–wortmani* is eliminated from these calculations because it is morphologically intermediate between *H. paulus–paulus* and *H. minusculus* and may represent biologically these two species at a very early stage.

For purposes of comparison with contemporaneous mammals, the Wasatchian Land Mammal Subage will be assumed to be six million years in duration (following figures 4.2–4.4 of Krishtalka et al., 1987). Four taxa of *Hyopsodus* evolved during this interval; this is an average and assumes *H. simplex* and *H. minor* are "conspecific" and that *H.* sp., cf. *H. mentalis* is a distinct taxon in at least some of its referred distribution. The corresponding evolutionary rate is approximately 0.67. In light of the fact that this calculation does not account for lineage segments, it is best compared with the first estimate given in the preceding paragraph. This rate would not contradict the data of Gingerich (1974*a,* 1976*b*), assuming each of his tooth size lineages represent taxa similar to the species of this study. It has already been noted that dental evidence conflicts with Gingerich's implied relationships in some cases, although the **number** of lineages is similar. The North American "Adapidae," according to Gingerich (1979), seem to comprise four or five lineages in the Wasatchian and early Bridgerian as well. Taxonomic debates concerning the specific and generic assignments and implied taxonomy of these primates will continue (K. C. Beard, personal communication); however, the overall evolutionary rate and pattern of M_1 size change are analogous to that seen in *Hyopsodus.* Another possible connotation of this primate data will be discussed below. Krishtalka and Stucky (1985) report four lineages of *Diacodexis* in the Wasatchian, three showing relationship to the stem lineage *Diacodexis secans,* a rate of cladogenesis similar to that of *Hyopsodus. Hyracotherium,* a mammal as abundant as *Hyopsodus,* has not been revised through the entire Wasatchian since Kitts (1956). Unfortunately, this revision of *Hyopsodus* is not directly comparable—Kitts believed that only upper premolar morphology was valid for taxonomic assignment and apparently only 500 or so specimens (this cannot be directly ascertained) were included in his analysis. Nevertheless, Kitts documented three species of *Hyracotherium* as well as five distinct subspecies marking temporal or geographic separation. The relationships of these taxa may be interpreted as representing three lineages: the large-sized *Hyracotherium craspedotum,* the smaller-sized *Hyracotherium angustidens/Hyracotherium vasaccience* lineage, and a *Hyracotherium vasaccience/venticolum/Orohippus* lineage (Kitts, 1956:55–57). The pattern of *Hyracotherium* lineage distribution through the Wasatchian is akin to that of *Hyopsodus,* as is the atypical size distribution of *Hyracotherium* reported by Kitts in the San Juan Basin horizons.

It has already been noted that several early Eocene omomyid primates show gradual change in dental morphology through time (Bown and Rose, 1987).

In contrast to these gradualistic patterns, a more abrupt dental evolutionary rate is evident in the artiodactyl *Bunophorus* (Stucky and Krishtalka, 1990) and the tillodont *Esthonyx* (Gingerich, 1980), for example. However, the number of specimens available for these revisions was only five percent of that known for *Hyopsodus.*

Hyopsodus may well be one taxon that, because of its abundance in the Eocene record, lends insight into change in mammalian dental morphology through time. As is often the case, greater knowledge in one area raises other questions of equal or greater magnitude. Would phylogenetic systematics have identified the emergent pattern of *Hyopsodus* evolution? In this case, it is clear that a cladistic analysis would not have done so. The integrity of a well-documented intermediate-sized lineage (one of the most commonly occurring fossil mammals known to paleontology) would have been broken into sister-group relationship with each of the *end members* of its various descendants. It would not remain a taxonomic entity, and the pattern of anagenetic evolution would have been lost or obscured.

Without critical understanding of the meaning and structural complexes of characters in their evolutionary context, cladistic analysis remains an exercise in gathering unrelated numerical data (Szalay, 1993). Evolutionary relationship and, therefore, phenetic distance is implied every time a character is thoughtfully weighed or assessed as primitive or derived. Without character assessment, cladism would merely be numerical taxonomy. Therefore, the "impartial data" resolved on cladograms *already* contains opinions of evolution. Gould (1991) seeks to resolve similar dilemmas by calling for the quantitative definition of morphospace, but gives no method of procedure. While this would undoubtedly resolve issues, it is probably a goal out of the paleontologist's present reach.

There is no method of quantitatively measuring a character's importance in reflecting phylogeny. "Consistency" or "retention" indices do not record change in size, shape, complexity, or location over time. Since this magnitude cannot be numerically assessed, the absolute number of characters supporting phylogenetic relationship also has little meaning. Character analysis and identification (before they are "counted") are still in the qualitative—and, arguably, evolutionary—state at this time. For example, it seems reasonable at least to hypothesize that if *Hyopsodus* were a primate, generic distinctions would be made among phena considered "species" in this review. It may be that Gingerich's (1979) "Adapidae" and *Hyopsodus,* showing similar phylogenetic pattern, responded similarly to similar selection pressures, and thus should be considered comparable early Eocene biologic entities.

Should change be expected to be equal for comparable biologic units? Does the degree of change have systematic importance? For example, does the loss of a premolar in a primate taxon phyletically equal the inflation of M_{1-2} entoconid and hypoconulid in *Hyopsodus powellianus*? Is it more or less taxonomically important? Without common definition, it is difficult to ascertain whether fossil phena are genera, species, regional variants, or even equivalent.

The phylogenetic pattern of *Hyopsodus* begs the question: what biological process is actually being documented in studies of fossil organisms from basins that, while isolated, are in close approximation with one another? This will have to remain uncertain, but does not change the fact that a common pattern does exist. If, as this author suspects, this change represents gradual population genetic shifts around a constrained mean, with small scale immigrations of new taxa representative of cladogenetic events, does this still not represent an important evolutionary phenomenon? Simply because the pattern is termed anagenetic at this level of resolution does not have to imply the presence of sympatric speciation. The paleogeography of Eocene western North America indicates excellent isolating basins for small scale allopatry. Change does occur—*Hyopsodus* from Lysitean localities does not look like *Hyopsodus* from Bridgerian localities, even if little apparent cladogenetic evolution has occurred in this interval. Interesting things are happening more or less concurrently in other basins. Examination of *Hyopsodus* from new collections from the Uinta Basin (K. Doi, University of Colorado, personal communication) documents different "micropatterns" in *Hyopsodus* evolution. For example, large Washakie *Hyopsodus* seems to reduce accessory cusps rather than enlarge them.

The most valuable conclusions of this report are not the synonymies or the proposed relationships of the taxa of *Hyopsodus*. Rather, they are the observations of the variation in dental characters, the change in frequency of these characters, and the evolutionary pattern they suggest. The pattern of *Hyopsodus* evolution was not inferred after an "impartial" cladistic analysis but after the construction of a character evaluation grounded in a sequential, temporal lattice (see functional–adaptive analysis in Bock, 1981). Virtually no character was unequivocally exclusive to a specific *Hyopsodus* taxon. Relative time suggested pattern. Without it, no character could be unquestionably evaluated and weighed.

This study is therefore the result of the same type of phylogenetic evaluation employed by workers since the advent of paleontology. That is, the inspection of material in its temporal context, gain of a qualitative knowledge of the frequency and importance of morphologic features, and the inference of a pattern of change in this morphology (Szalay, 1993). These analytical threads are still basic to paleontological technique. Taxa defined by common principles can only improve the results of integrated studies of evolution, biostratigraphy, and paleoecology.

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